ORIGIN, PHYLOGENY AND CLASSIFICATION OF THE PHYLUM MOLLUSCA

ORIGEN, FILOGENIA Y CLASIFICACION DEL PHYLUM MOLLUSCA

Luitfried v. Salvini-Plawen*

Key Words: Origin, phylogeny, classification, Mollusca.
Palabras Clave: Origen, filogenia, clasificación, Mollusca.

ABSTRACT

New investigations and insights of molluscan research with respect to origin, evolutionary pathways and systematic consequences are presented and discussed within the framework of previosly advanced concepts. Due to their primitively aplacophoran configuration, their small size and lack of planktotrophy, it is demonstrated that the derivation of the Mollusca from a small, plathelminthomorph organisation becomes more and more plausible *versus* a coelomate origin. Several interdependent trends in organ elaboration allow the subsequent anagenetic differentiation and radiation within the phylum to be most consistently outlined along the successive levels of aplacophoran, polyplacophoran and monoplacophoran configuration; the higer Conchifera branch into the clades of Loboconcha (Bivalvia, Scaphopoda) and Visceroconcha (Gastropoda, Siphonopoda = cephalopods). The relevant main events and synapomorphies are presented and implemented in classification.

INTRODUCTION

The molluscs are the third most numerous animal group (an estimated 50000 species; *cf.* BOSS, 1971, 1982) after the insects and vertebrates. Moreover, their evolutionary radiation brought about considerable diversification during phylogeny. This is systematically recognized today in the form of eight extant and several extinct classes within the three anagenetic levels of aplacophoran, polyplacophoran and monoplacophoran (= conchiferan) organization. Consequently, and because of the immense ecological and structural variability (body sizes range between 0.3 mm and 8 m), the phylum Mollusca can only be defined by the combination of several characters or even organ systems. In contrast to many familiar representations dominated by conchiferan organization (in nearly all textbooks, *e.g. Fig.4*), neither a shell or a distinct tripartition into head, foot and visceral body is characteristic for "the" molluscs (*cf.* SALVINI-PLAWEN, 1985). Rather, the Mollusca are defined as soft-bodied spiralian Gastroneuralia with[1] the dorsal epidermis (mantle or pallium) covered by cuticular and/or calcareous secretions;[2] the ventral body elaborated into a perioral head region and a ciliar to muscular locomotory organ;[3] a pallial cavity housing lamellate gills (ctenidia), a pair of mucous tracts, and the body outlets;[4] a tetraneurous nervous system (though often concentrated) and a paired chemoreceptive (osphradial) sense organ;[5] a dominant dorsoventral muscle system;[6] a series of pharyngeal teeth (radula; though partly reduced);[7] a haemolymp-

* Institut für Zoologie der Universität A-1090 WIEN IX, Althanstraße 14, Austria.

1

hatic body cavity; and[8] a gono-pericardial complex (often including an excretory system).

Another consequence of such diversity involves the recognition, reconstruction and interpretation of the origin, phylogeny and classification of the Mollusca. Historical preconceptions, the predominance of quantitative data in scientific studies or specific viewpoints of specialists and nonspecialists have constructively or misleadingly contributed to a manifold spectrum of in part controversial views. More recent information in different fields of malacology, however, allows us to outline the present status of knowledge and to arrive at a more accurate survey.

A) ORIGIN

A long-lasting debate about the origin of the molluscan phylum focuses on the organization of the body cavity of the forerunners: Was it mesenchymate as in flatworms or was it of a coelomate (homogeneous or even segmented) construction? Which new arguments favour one or the other alternative? And what functional and/or ecological considerations can be contributed?

1) General organization

Earlier considerations in the direction of coelomate segmentation in molluscs have been discussed at length and refuted by HOFFMANN (1937). The discovery of living Tryblidia has renewed, however, the interpretation of primarily segmented Mollusca (LEMCHE & WINGSTRAND, 1959; GUTMANN, 1974; GÖTTING, 1980; WINGSTRAND, 1985; GHISELIN, 1988); this in turn was critisized and contradicted by VAGVOLGYI (1988), SALVINI-PLAWEN (1968, 1972, 1981a, 1985, 1988b), RUSSELL-HUNTER (1988) or WILLMER (1990). Accordingly, neither traditional views based on dated information, nor the serial repetition of various organs (mutually being out of a common phase), nor the organization of aplacophorous molluscs (widely neglected) favour the view of metameric molluscan ancestors. This argumentation is supported by the three following comparative aspects.

(1) More recent comparative studies of the primarily shell-less Caudofoveata and Solenogastres (summarized in SALVINI-PLAWEN, 1985) demons-

trated certain distinct trends in molluscan evolution: The Mollusca are characterized by an additive increase in complexity (by functional-morphological sequences) in the elaboration of the mantle cover, the musculature, the alimentary tract and of sensory organs (see below). These sequences interconnectingly reflect phylogenetic pathways (SALVINI-PLAWEN, 1981 a, 1985); they allow the establishment of the "lowest common denominator" of respective organ systems and enable basic molluscan organization to be traced.

(2) Rather than possessing a secondary body cavity (= body coelom), the Mollusca have a special gono-pericardium elaborated from part of the 4 d material in (function-conditioned) divergence to the body coelom in Echiurida-Annelida (cf. VAGVOLGYI, 1967; SALVINI-PLAWEN, 1968, 1972, 1981a; STASEK, 1972; CLARK, 1979; WILLMER, 1990). Also the molluscan pericardioducts cannot be homologized with coelomate metanephridia (cf. SALVINI-PLAWEN 1988 b), the more since the latter represent reorganized protonephridia (BARTHOLOMAEUS, 1990) primarily not existent in Mollusca. On the other hand, the body coelom as a hydrostatic organ is correlated with infaunal (burrowing) locomotion (cf. CLARK, 1964). In molluscs, however, conservative groups and/or those with small-sized animals generally show a muco-ciliary gliding; this contradicts a secondary body cavity (there is no requirement for it) and supports the gono-pericardium as a differentiation suis generis (cf. TRUEMAN, 1975).

(3) A locomotory body coelom is indicative of relatively large organisms; ciliary gliding in conservative or small-sized molluscs should therefore represent a secondary state (cf. GUTMANN, 1974) if they were of coelomate ancestry (as for example, in the 'archiannelids'). Depending on the weight of an animal in the external medium (mass/volume), the size limit for muco-ciliary locomotion ranges between "a few millimeters" and about 11 mm (TRUEMAN, 1975: 18-19). RUNNEGAR & POJETA (1985: 11-12) already emphasized the small body size of Cambrian conchiferan molluscs (e.g. the earliest bivalves Pojetaja = 1 mm, Fordilla = 2-5 mm), while CHAFFEE & LINDBERG (1986) demonstrated that early Cambrian Conchifera measured only 1-2 mm. Moreover, the Precambrian and early Cambrian Placophora described by YU (1987) from China were like-wise small (1.2
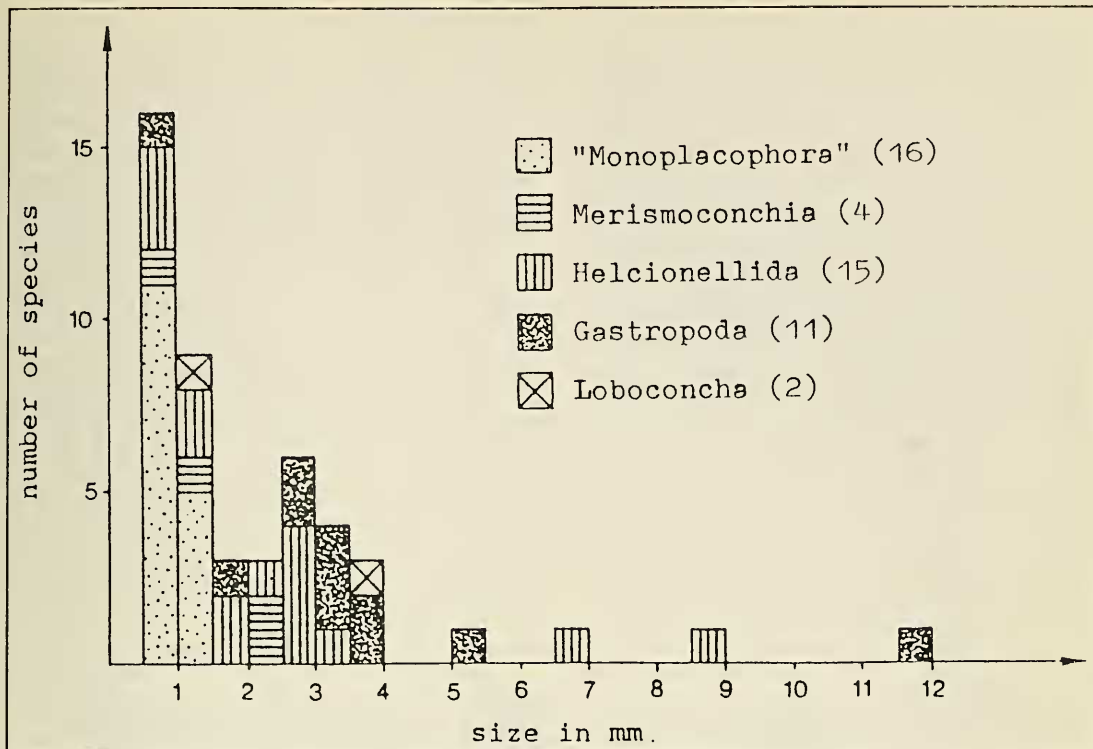
Fig. 1. Size distribution of the "Yangtze molluscan fauna" including 48 conchiferan species from earliest Cambrium (compiled by G. HASZPRUNAR according to data from YU, 1987; the maximum size of each species is provided).

mm - 5 mm); most conchiferan shells from the earliest Cambrium in China range between 0.5 mm and 4 mm (Fig. 1). Among extant molluscs, the most conservative members (order Pholidoskepia) of the muco-ciliarity gliding Solenogastres predominantly include 1-4 mm long species.

2) Developmental characters

Developmental similarities such as spiral cleavage with cross formation ('molluscan' cross also in sipunculids), the elaboration of apical plate and trochi (see "Trochophora"), or the proliferation of ento-mesoblastic bands out of the 4 d blastomeres have often been interpreted as evidence for a common coelomate or even annelid ancestry of the molluscs. None of these characters, however, withstand critical scrutiny: these similarities are either valid for the common level of Spiralia or they turn out to represent functionally-conditioned convergencies (cf. VAGVOLGYI, 1967; SALVI-NI-PLAWEN, 1968, 1972, 1980b, 1985, 1988b; WILLMER, 1990).

Planktotrophy in molluscan larvae is apparently secondary (convergencies). According to OLIVE (1985), planktotrophic development is ecophysiologically correlated with large bodies, if fertilization is external. External fertilization, again, is considered by FRANZEN (1956, 1970) and WIRTH (1984) to be the original condition in molluscs' ("primitive type" of sperm). The small size of early molluscs (see above) thus indicates that larval development (Fig. 2) proceeded from non-planktotrophic but lecithotrophic (see pericalymma and pseudotrochophora larvae) to planktotrophy and thus shows planktotrophic larvae (see rotigers, veligers) to be secondarily derived (CHAFFEE & LINDBERG, 1986).

Functionally-conditioned convergencies especially hold true for larval types, uncritically termed Trochophorae. It has been demonstrated (FIORONI, 1966, 1982; SALVINI-PLAWEN, 1972, 1980b,

1988b) that the Pseudotrochophora (or 'praeveli-ger') in Mollusca, the Trichosphaera in Sipunculida, and the true Trochophora in Polychaeta as well as Echiurida represent evolutionary successive, convergent organizations of a basic Pericalymma type of larva. These larvae —with apical plate and ciliary tuft— are characterized by a large episphaeral cover (calymma) of ciliated cells which envelop the growing pre-adult organism. Termed test-cell larva in Mollusca (Fig. 2), Endolarva in Polychaeta, and serosa-larva in Sipunculida, they are primitively lecithotrophic, short-range larvae without fuctional gut or anus (cf. CHANLEY, 1969; MINICHEV & STAROBOGATOV, 1972; SALVINI-PLAWEN, 1980b). In more advanced molluscs (Fig. 2), the cell-cover was successively reduced in convergence to a broad girdle of cells (Stenocalymma type) and to a prototroch (Pseudotrochophora, without nutritive metatroch; cf. also CHAFFEE & LINDBERG, 1986). Finally, however, planktotroph nourishment was enabled by secondary velar enlargements: in Rotigers (autobranch Bivalvia) the nutritive ciliation is newly-formed (not derived from true trochus cells, cf. ERDMANN,
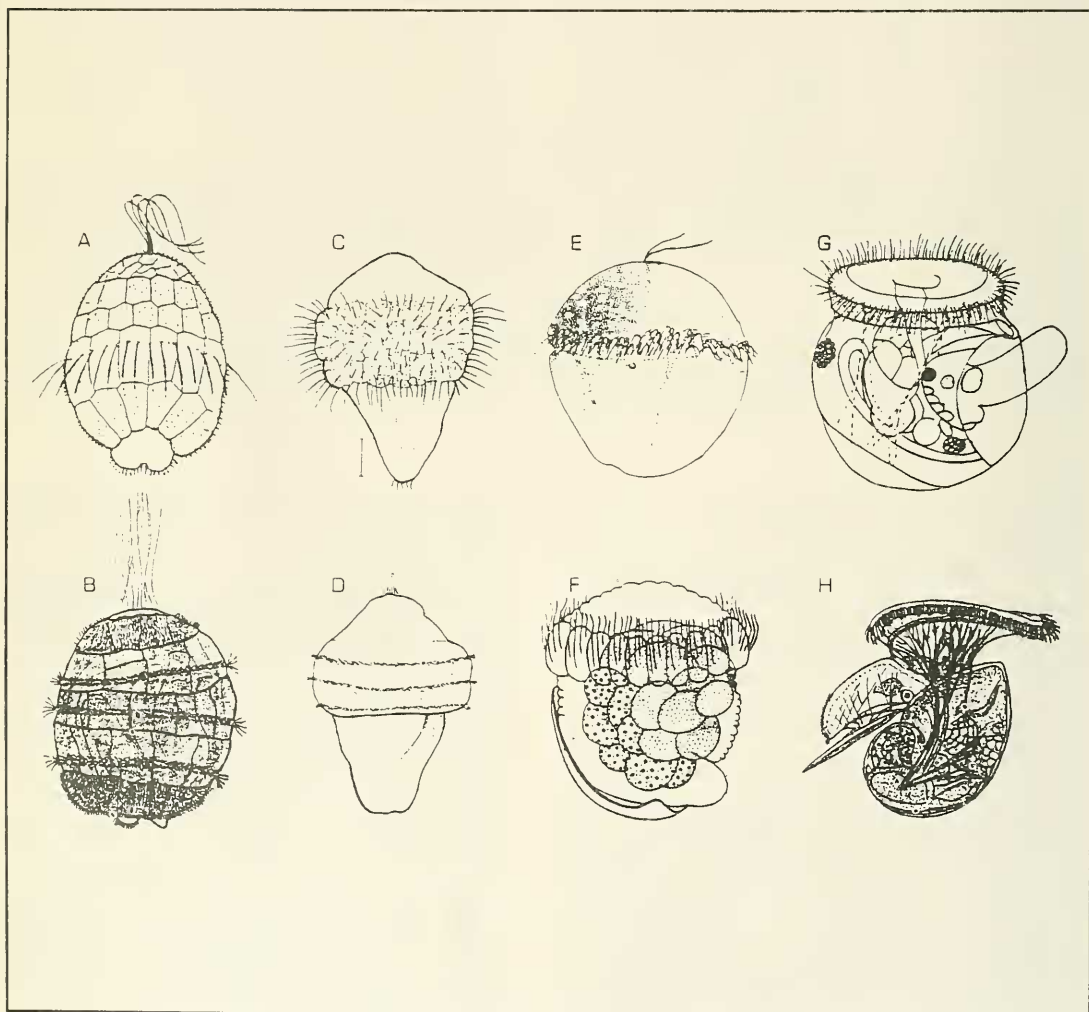

Fig. 2. Types of molluscan larvae. A & B - Pericalymma type/test-cell larva: A = *Neomenia carinata* (Solenogastres; after THOMSON, 1960); B = *Nucula proxima* (Bivalvia-Ctenidiobranchia; after DREW, 1901); C & D - Stenocalymma type: C = *Scutopus robustus* (Caudofoveata; courtesy of W. PEKNY, Wien), D = *Dentalium* (Scaphopoda; from KOWALEVSKY, 1883); E & F - Pseudotro-chophora type: E = *Stenoplax heathiana* (Placophora; from HEATH, 1899); F = *Haliotis tuberculata* (Archaeogastropoda; after CROFTS, 1937); G = Rotiger larva of *Ostrea edulis* (Bivalvia-Autobranchia; after ERDMANN, 1934); H = Veliger larva of *Crepidula fornicata* (Caenogastropoda; from WERNER, 1955).

1934: Taf. 2, Abb. 4) and in Veligers (higher Gastropoda) the nutritive ciliation is part of the preoral prototroch (*cf.* WERNER, 1955: Abb. 8). In turn, in polychaetes the mouth opening obviuosly broke directly through the calymma, leaving the preoral ciliation as a locomotory prototroch and the resulting postoral ciliation of the calymma as a nutritive metatroch (SALVINI-PLAWEN, 1980b).

3) *Palaeontology*

There are no fossil records of Caudofoveata or Solenogastres. Owing to the purely aragonitic composition and rather delicate structure of the mantle scales and spicules in both groups, fossilization (wich high pressures) of these elements may occur only under most favorable conditions. The trace fossil *Bunyerichnus dalgarnoi,* described from a 21-33 mm wide, ribbon-like trail with median ridge and regular transverse grooves, obviously used "rhythmic muscular contractions" (GLAESSNER, 1969: 376-379). Such locomotory behaviour, however, is not related to Neomenioidea (= Solenogastres) as advanced by GLAESSNER, since Solenogastres exclusively employ mucociliary tracts. *Wiwaxia corrugata,* the sclerites of which suggest aplacophoran affinities and the feeding apparatus resembling certain gastropod jaws or nudibranch radulae (rather than primitive radulae, *cf.* p. 11), has also turned out to be no mollusc (RUNNEGAR & POJETA, 1985: 47; CONWAY MORRIS, 1985: 566-569; CONWAY MORRIS & PEEL, 1990). On the other hand, the Conodonta, interpreted by TILLIER & CUIF (1986) and TILLIER & JANVIER (1986) to represent buccal armatures (radula and "mandible") of Caudofoveata, show merely superficial similarities (BRIGGS *et al.,* 1987).

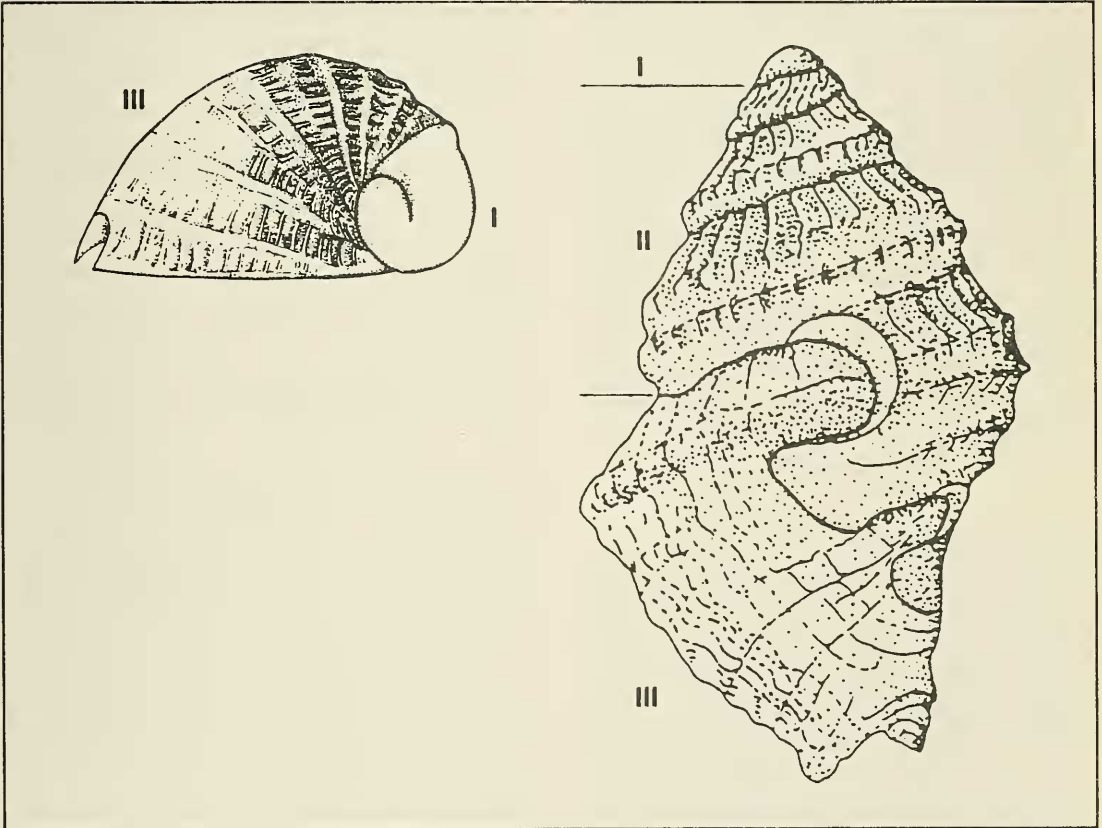Other molluscs, i.e. both Placophora and Con-

Fig. 3. Gastropod shells. Above = juvenile *Emarginula tuberculosa* (Archaeogastropoda-Vetigastropoda); to the right = juvenile *Thais haemastoma* (Caenogastropoda): I = embryonic shell; II = larval shell correlated to planktotrophy; III = adult shell (after BANDEL, 1982).

chifera, are represented in the fossil record from the earliest Cambrium, some 570-550 million years ago (RUNNEGAR & POJETA, 1985; YU, 1987). Apart from relationships and phylogenetic inter-connections within the conchiferan classes, the fossil record provides little clue as to the origin of the molluscs or how the eight extant classes diffe-rentiated in Precambrium times. The frequent argumentation that the late stratigraphic occurren-ce of Placophora contradicts their primitiveness and their ancestry to conchifera has been anulled (*cf.* YU, 1987); this is also true of the discussion on the organisation of *Mathevia* as representing "the oldest chiton" (RUNNEGAR & POJETA, 1985: 46-47; SALVINI-PLAWEN, 1985: 111).

Due to preservation of embryonic and larval shells down to the early Triassic, however, the larval biology of Conchifera can even be traced in the extinct species (JABLONSKI & LUTZ, 1983; CHAFFEE & LINDBERG, 1986; LIMA & LUTZ, 1990): The elaboration of the concha begins with a small, cap-shaped primary shell (= embrionic shell = protoconch I = prodissoconch I), whose size is correlated to the amount of yolk in the egg (*cf.* SHUTO, 1974). A multi-whorled secondary shell (= larval shell = protoconch II = prodissoconch II), however, is only produced in organisms with lar-val planktotrophy (Fig. 3; *cf.* SHUTO, 1974; BANDEL, 1982). Since the tertiary shell (= adult shell = teleoconch), secreted during or after meta-morphosis, is preceded solely by the primary/embryonic shell in members of primitive gastro-pod as well as early bivalve branches, it can be assumed that these extinct representatives likewi-se lacked planktotrophic larvae (see above).

4) *The molecular approach*

At first glance, most of the above evidence seems to be contradicted by results of the molecu-lar approach, especially those dealing with mo-lluscs proper as in GHISELIN (1988). These inves-tigations are based upon 18S rRNA molecules and propose an origin of the Mollusca from segmented coelomates (GHISELIN, 1988: Table 1). However, some data were eliminated as convergences be-cause of morphological (!) evidence for monophyly of Mollusca, Arthropoda (*versus* MANTON & ANDERSON, 1979; or WILLMER, 1990), Echino-dermata and Chordata (GHISELIN, 1988: 77/78).

Yet, what would have been the results if, for exam-ple, (a) the molluscs had not been regarded *a priori* as a natural group, or (b) the Articulata (Annelida + Arthropoda) or Deuterostomia in contrast had been handled as monophyletic groups? Thus, for some selected, traditionally monophyletic groups euphemistic premises are made, for others not. In addition, "no reliable evidence for a relationship among the Eutrochozoa" (i.e. annelids, sipuncu-lids, and molluscs) was available, but at most "a sister-group relationship between Mollusca and Annelida s.l." with a possible synapomorphy for molluscs and sipunculids (GHISELIN, 1988: 79). The molecular data then would be consistent with the developmental characters presented above (*cf.* SALVINI-PLAWEN, 1988b). GHISELIN himself (1988: 79-81) discusses other possible alternati-ves. As a whole, the data by no means directly support the phylogenetic diagram presented by GHISELIN (1988: Table 1); rather, the latter ap-pears to selectively include only those data agreeing with the author's views of (morphologically-ba-sed) relationships.

The mollusc results in the more general study by FIELD *et al.* (1988: Fig. 5) are those presented in more detail by GHISELIN (1988) and thus share the same problems. Other conclusions appear to be no more reliable, since they are all only based on a few percent differences in sequence divergence. Fi-nally, recent investigations depreciate most phylo-genetic reconstructions based on 18S rRNA se-quences in taxa which "have diverged more re-cently than about 100 Ma", or at most up to 250 Ma (SMITH, 1989: 321). This excludes all relations-hips dating from the Palæozoic or even prior to the Cretaceous, i.e. the origins of all molluscan clas-ses. The approaches to phylogeny using 5S rRNA (*cf.* HENDRIKS *et al.,* 1986) apparently suffer from similar problems and the fairly chaotic results have already been rejected by GHISELIN (1988: 74). GHISELIN (1988: 71) also points to the weak-ness of the sequence data of the cytochrome c molecule; this critique may also be applied to the model by BERGSTRÖM (1986; with extreme polyphyly of the body coelom), who likewise uses the problematic data of LYDDIATT *et al.* (1978). The structure of haemoglobin molecules and their occurrence (*cf.* TERWILLIGER, 1980) also provide no relevant information. The presence or absence of phosphagene molecules (WATTS, 1975) may

indicate a common ancestry for molluscs, sipun-culids and annelids; neither these nor other bioche-mical data, however, have been helpful in tracing molluscan origin (cf. SALVINI-PLAWEN, 1988b; WILLMER, 1990: 78-87).

As a consequence, the molecular approach remains ambiguous or is even negative. This may either be due to a high rate of "convergent solu-tions to similar requirements for molecular func-tioning" at all systematics levels (WILLMER, 1990: 99), or it may reflect the sparse material investiga-ted with respect to character hierarchy. Broader investigations beginning with sequences and struc-tures of molecules in ecophysiologically different representatives of successive systematic catego-ries (genera, families, orders, classes) are required to discover up to which hierarchic taxon the res-pective results are reliable (see also SMITH, 1989). Only such a wide-ranging spectrum for two or more phyla could reveal inter-phyletic relations-hips. Similar strategies involving character relia-bility in ultrastructural research have been highly informative with respect to the intra-phyletic fra-me (e.g. HASZPRUNAR, 1985b, 1987a-b).

5) Conclusions

Within the Gastroneuralia, the Mollusca share with some other Spiralia a pair of cerebral ganglia and longitudinal, medullar body nerve cords, a stomogastric system, spiral cleavage, or the blas-tomere 4 d proliferating the ento-mesoblast; such characters are therefore plesiomorphic. Closed relationships appear to exist with the Sipunculida (cross of blastomeres, larval calymma) and with the Echiurida-Annelida (SALVINI-PLAWEN, 1988b). In both cases this is, however (and in constrast to GHISELIN, 1988, for example), indica-ted only by the lecithotrophic Pericalymma type of larvae (and by cell-junctions? cf. GREEN & BERG-QUIST, 1982), and is also consistent with the serio-logical results of WILHELMI (1944). Such synapo-morphies have no affect on the conditions of the body cavity in the adult — all the more since (as must be stressed) neither the small size nor the locomotory behaviour of the original molluscs favoured or even required a body coelom. Rather the muco-ciliary gliding, the mesenchymate cons-truction including dorsoventral musculature, or the morphogenesis of the nervous system appear

to be plesiomorphically inherited characters from the plathelminthomorph level.

These conditions reveal that all coelomate Spi-ralia —as a monophyletic clade— represent the sister-group of the Mollusca (SALVINI-PLAWEN, 1988b). The coelomate clade (sipunculids, echiu-rids, and annelids; rather than annelids alone) most probably deviated by adapting to an infaunal manner of living (circular cross section, body coelom); this contrasts to the molluscan line, which retained the ciliary-gliding, mesenchymate orga-nization but adapted the mantle cover.

B) PHYLOGENY

During the last decades investigations on diffe-rent aspects of molluscan biology, including stu-dies on the primary shell-less groups, have also provided new insights into phylogenetic affinities. The most consistent item in this respect are func-tionally-orientated considerations, with a general withdrawal from a conchiferan archetype (though still propagated in text-books, see Fig. 4) and the discernment of an aplacophoran origin with diffe-rentiation on subsequent levels (e.g. YONGE, 1947 vs. STASEK, 1972). This stems from the insight that several sequences in elaboration of organ systems overlappingly determine the evolutionary direc-tion of whole synorganized organization. In con-nection with molluscan origin, this allows the organization of the initial archimollusc population to be outlined (see Fig. 9) and anagenetic radiation of the phylum to be displayed.

1) Sequences in organ systems

New knowledge about the aplacophoran groups (summarized in SALVINI-PLAWEN, 1985) and the comparative re-evaluation of their organization has yielded important information on the evolutio-nary pathway of the Mollusca as a whole. This approach involves analyzing the configuration of these organ systems which underwent distinct sequences of modifications.

(a) The most obvious elaboration is the mantle (Fig. 5). It differentiated from an aculiferan confi-guration with a cuticular cover and embedded cal-careous bodies, to an aculiferan mantle middor-sally replaced by serial calcareous plates, to a
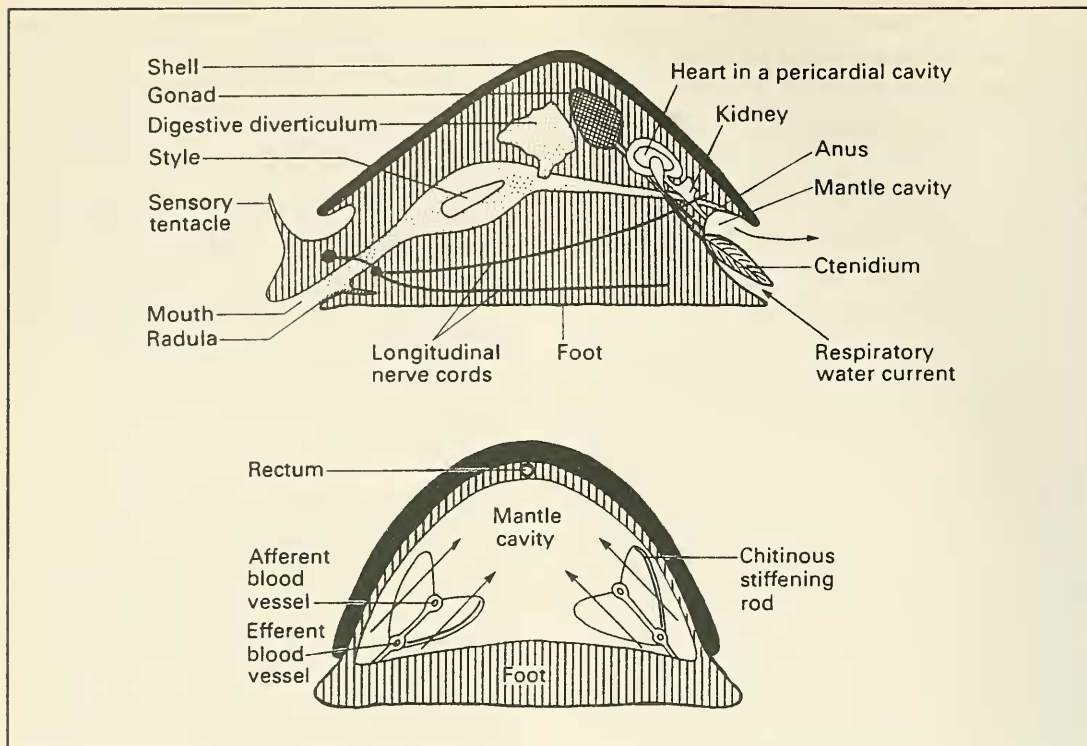
Fig. 4. "Generalized basic mollusc" (above = diagrammatic longitudinal section; below = cross-section through mantle cavity) after BARNES, CALOW & OLIVE (1988); this clearly refers to conditions based on gastropod characters only (cf. YONGE, 1947). In contrast, compare with Fig. 9.

mantle covered by a homogeneous shell (out of eight fused plates; cf. HAAS, 1981).

(b) The mantle in Caudofoveata and Solenogastres is equipped with epidermal papillae piercing the cuticle. Comparable mantle papillae exist as (photoreceptive) aesthetes and girdle papillae in Placophora. Several Conchifera of more primitive levels, however, possess also mantle papillae enclosed within the shell (cf. SALVINI-PLAWEN, 1985: 115); this supports a hereditary condition.

(c) The mantle cavity primitively housed (one pair of) ctenidia, mucous tracts, and the body outlets (Fig. 5). The mucous tracts appear to be conservatively configurated in Placophora, but are turned upside-down in Caudofoveata and internalized in Solenogastres (spawning ducts; cf. HOFFMAN, 1949). In primitive Bivalvia the configuration of the 'hypobranchial glands' corresponds to that in Placophora (Fig. 5), whereas the mucous tracts are somewhat restricted in Tryblidia, retai-

ned as nidamental glands in Siphonopoda (= cephalopods), and modified as hypobranchial glands at the roof of the mantle cavity in Gastropoda (see p. 16, and SALVINI-PLAWEN, 1972, 1981a).

(d) In all Mollusca the ventral body is subdivided by innervation into two regions, i.e. into a cerebrally-inervated perioral region and a ventrally-innnervated pedal region.[1] In Caudofoveata the cerebrally-innervated post-oral epithelium forms a plate or shield (see p. 19) with sensory and gland cells, the latter opening intercellularly either in a scattered distribution (Fig. 6) or being concentrated along the shield margins. This corresponds to the condition of the ventrally-innervated locomotory surface in Solenogastres (Fig. 7) and might well represent the cerebrally-innervated, anteriorly separated and somewhat modified remainder of a previously extensive locomotory surface (cf. HOFFMAN, 1949; SALVINI-PLAWEN, 1972: 294-304, 1985: 66). The shield is provided with long inter-
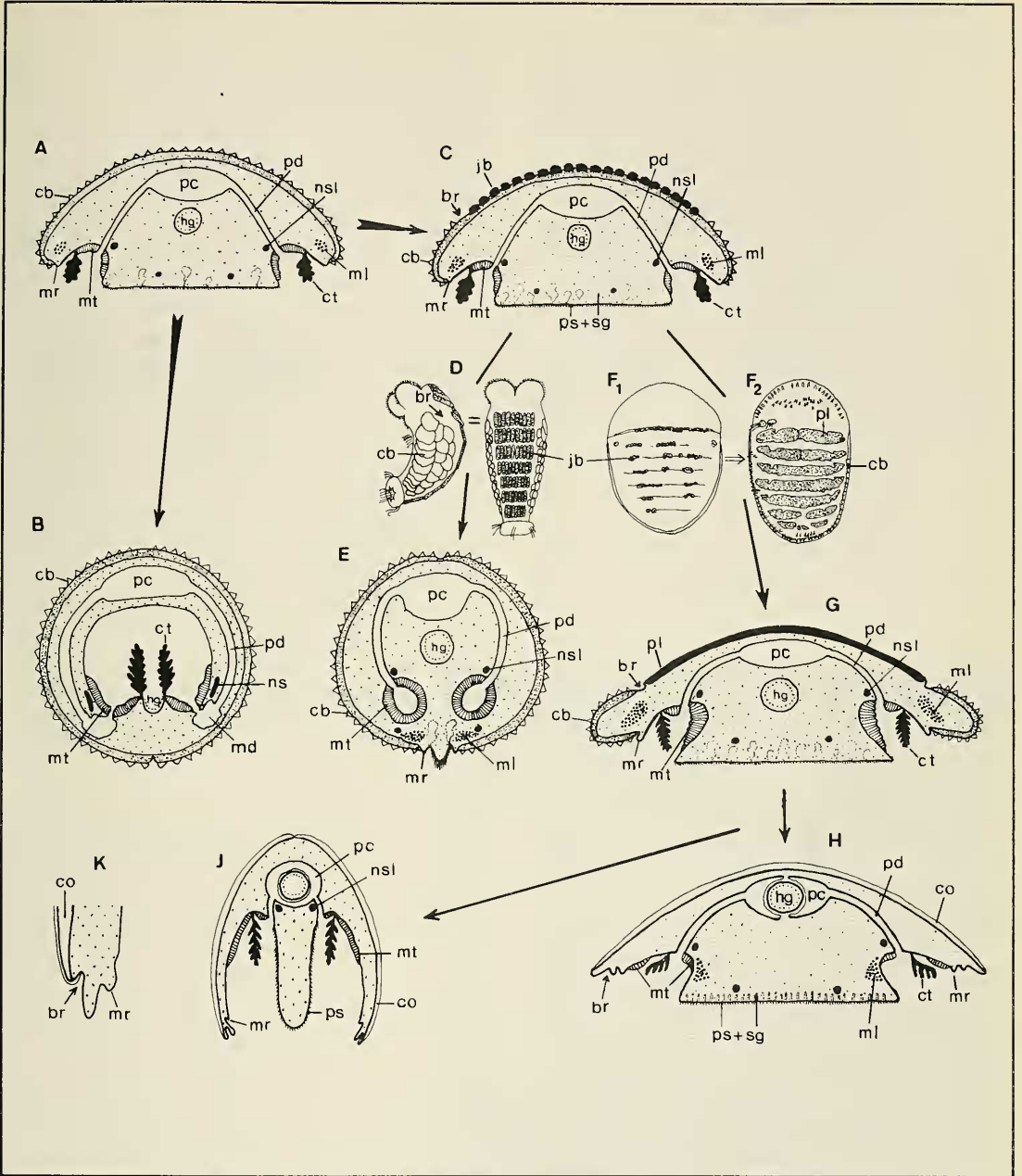
Fig. 5. Relationships among Mollusca according to the conditions of the mantle cavity, the mantle cover, and the pericardioducts (after SALVINI-PLAWEN, 1981a and 1985). A: Molluscan archetype; B: Caudofoveata; C: Heterotecta (common type ancestral to Solenogastres and Placophora); D: Solenogastres (late metamorphosis stage of *Nematomenia banyulensis* Pruvot); E: Solenogastres (adult); F: Placophora (two successive stages of just metamorphosed *Middendorffia polii* Philippi); G: Placophora (adult); H: Tryblidia; J: Bivalvia-Ctenidiobranchia; K: Siphonopoda (mantle border of *Nautilus*). (br = Break (= periostracal groove) between the mantle portion producing regularly-arranged calcareous bodies or valves or concha respectively and the peripheric portion whith irregularly-arranged bodies or girdle or middle mantle fold respectively; cb = irregularly-arranged calcareous mantle bodies; co = concha (shell); ct = ctenidium; hg = hindgut; jb = calcareous bodies regularly-arranged in seven transverse rows; md = glandular duct; ml = longitudinal muscle; mr = mantle rim (inner mantle fold); mt = mucous tract; ns = (fused lateral and ventral) nerve cord; nsl = lateral (pleural) nerve cord; pc = pericardium; pd = pericardioduct; pl = valve (shell-plate); ps = pedal sole (foot); sg = sole glands).

digitating microvilli embedded in a granular, dense intercellular matrix or cuticle continuous with the foregut (SALVINI-PLAWEN, 1985: 66; TSCHER-KASSKY, 1989: 254). However, since the fine morphology of the shield and foregut epithelia are distinctly different (SCHELTEMA, 1981: 363-364; TSCHERKASSKY, 1989) and since the presence of the cuticle is secondary, these conditions do not effect the possible homology of the shield with an anterior portion of former locomotory surface (*cf.* SALVINI-PLAWEN, 1981b: 401, in contrast to SCHELTEMA, 1981: 378, 1988: 61).[2] The ventrally-innervated pedal region in Solenogastres, Placophora and Conchifera is principally provided with an anterior pedal gland (funnel gland in cephalopods); this defines these groups as Adenopoda in contrast to the Scutopoda (Caudofoveata). Whether these conditions also refer to evolutionary levels (pedal gland as a true synapomorphic character for recent Adenopoda alaone or for all Mollusca) cannot yet be accuralety evaluated (see also p. 19/20), since no organogenesis is known for Caudofoveata.[3] The peri-oral, cerebrally-innervated anterior region is differentiated in Testaria (Placophora and Conchiphera) as a head. Only Conchifera, however, show head appendages (including the "cephalopod" arms, *p. 20*).

(e) Correlated to mantle cover changes, the musculature underwent a specializing restriction from the aplacophoran level (two or three-layered subintegumental system, longitudinal-marginal system enabling a rolling up, and serial dorsoventral system), to the polyplacophoran level (restriction of the subintegumental system to the intervalve bundles and the restriction of the dorsoventral system to $8 \times 2 = 16$ pairs of bundles correlated to the eight mantle plates), to the level of Conchifera. The latter show a reduced subintegumental system, but the conservative Tryblidia still retain the paired longitudinal system (= *Musculus long. circularis pedalis; cf*. Fig. 5) and the octoserial dorso-ventral musculature. Other Conchifera in-

Fig. 6. Part of cross section through the pedal shield of *Scutopus ventrolineatus* Salvini-Plawen (Caudofoveata; courtesy of M. TSCHERKASSKY, 1989). (ci = base of cilium; gc = epithelial portion of gland cell; mu = underlying musculature; mv = interdigitating microvilli; nu = nucleus; ol = outer layer of granular matrix, devoid of microvilli; rc = receptor cell; sf = supporting fibre; ve = vesicles in distal cell portion; bar = 5 mm).
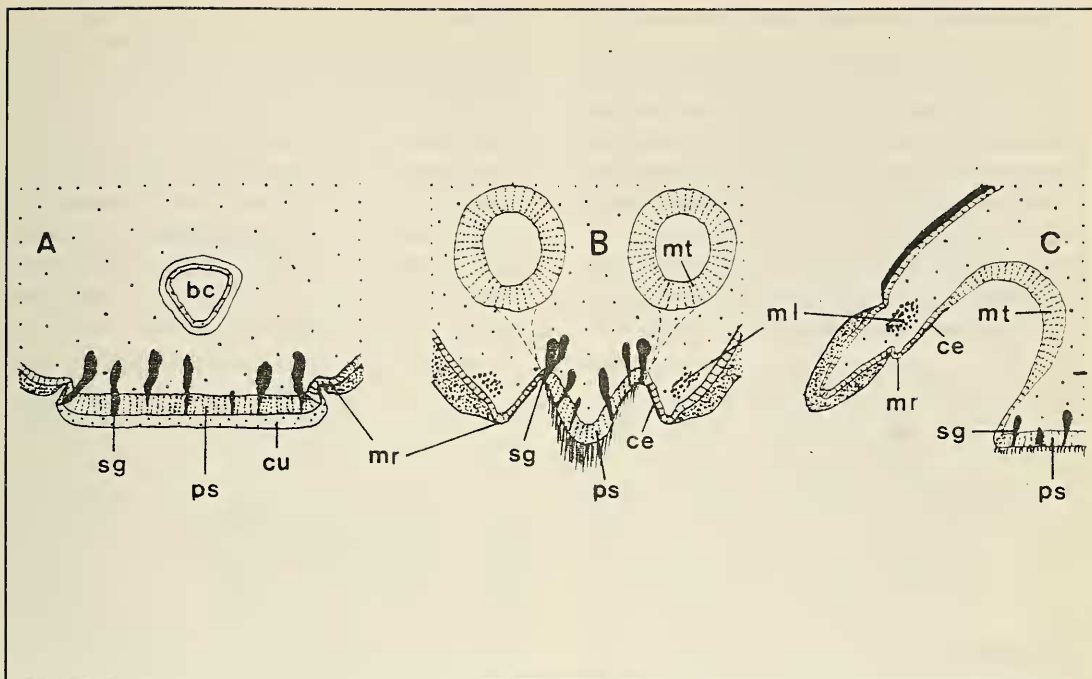
Fig. 7. Mantle rim and adjacent organs in *A* Caudofoveata (region of pedal shield), *B* Solenogastres (region of spawning ducts), and *C* Placophora (region of mucous tracts). (ce =purely microvillous epithelium of mantle groove; cu = layer of irregularly-arranged microvilli within matrix of glycocalix (see Fig. 6); mr = mantle rim (inner mantle fold); mt = mucous tract of mantle cavity; ps = cerebrally-innervated pedal shield or ventrally-innervated pedal sole respectively; sg = pedalshield/sole glands).

creasingly concentrate or restrict the dorso-ventral musculature to form the foot/shell retractors, the spindle/columellar muscle, or the cephalopod funnel depressors and head retractors (*cf.* SALVINI-PLAWEN, 1981a, 1985).

(f) The original foregut was characterized by a radula apparatus and two sets of associated glands only (bucco-pharyngeal glands and a pair of organs ventral to the radula). The radula appears to have primitively represented a monoserial organ consisting of a pre-ribbon with a lateral, cusp- or hook- like thickening serially at each side. Only later occurred a separation into a distinct ribbon (radular membrane) and into the inserted pairs of teeth (distich type). The latter condition is more generally considered consevative in molluscs (*cf.* KERTH, 1983: 266; SCHELTEMA, 1988: 67; SALVI-NI-PLAWEN, 1988a: 355-359), and likewise suggests carnivorous nourishment. In the still carnivorous Solenogastres the differentiation only advanced to an intermediate configuration since the teeth are not yet structurally and formatively

separated from the pre-ribbon (rudimentary ribbon, "basal cuticle"; *cf.* SALVINI-PLAWEN, 1988a: 312 & 355-359; WOLTER, 1991; also KERTH, 1983: 252). In some Placophora the ontogenetic differentiation of the radula (*cf.* SIRENKO & MINICHEV, 1975) appears to recapitulate such an evolutionary pathway. On the other hand, the radular operation in Placophora, Tryblidia and Scaphopoda is of the 'stereoglossate' condition as in docoglossan gastropods (*cf.* WINGSTRAND, 1985; SALVINI-PLAWEN, 1988a: 359); other Gastropoda exhibit the more advanced 'flexoglossate' condition.

(g) The entodermal alimentary tract (Fig. 8) originally included a wide, uniform midgut, such as still present in the Solenogastres (SALVINI-PLAWEN, 1988a). The Caudofoveata deviated by the longitudinal subdivision of the posterior midgut into a slender intestine and a single, voluminous, ventral midgut sac. A new type of midgut is differentiated in Placophora: an oesophagus with paired pouch (so-called sugar gland), a stomach

with a pair of midgut or digestive glands, as well as a long and somewhat coiled intestine. The Conchifera clearly inherited this configuration (Fig. 8), but at their common base the simple stomach was elaborated into a fairly specialized protostylesac stomach with subsequent modification depending on subclasse (SALVINI-PLAWEN, 1981b; 1988a).

(h) In Testaria (Placophora and Conchifera) the foregut is basically equipped with a newly evolved, chemoreceptive subradular sense organ. Only Conchifera, however, possess both jaw formations and statocysts; additional structures typical for Conchifera include a sub-rectal commissure and head appendages (SALVINI-PLAWEN, 1972, 1981a).

(i) Among Conchifera, only the Visceroconcha (Gastropoda and Siphonopoda = cephalopods) have a head set off from the mantle and shell; this free head is provided with cerebral photoreceptors. In addition, they possess a purely posterior mantle cavity, lateral/pleural nerve cords medial of the dorsoventral musculature, and an antagonistic three-dimensional muscle-on-muscle system

Fig. 8. Differentiation of the midgut in Mollusca (from SALVINI-PLAWEN, 1988a). A = Configuration in molluscan archetype; B = reorganization in Testaria (Placophora and Conchifera) with glandular oesophageal pouches and midgut glands; C = organization of stomach in Placophora and in Conchifera (protostyle-sac type); D = principal organization of stomach in recent molluscan classes; E = outline of midgut in recent molluscan classes.

(SALVINI-PLAWEN, 1985; TRUEMAN & BROWN, 1985; HASZPRUNAR, 1988: 404-405).

2) *The archimolluscan organization*

In concordance with the preceding argumentation and based on a broad comparative analysis of anatomical, ontogenetic as well as behavioural features (*e.g.* SALVINI-PLAWEN, 1972, 1985, 1988a; WINGSTRAND, 1985; HASZPRUNAR, 1988), the most primitive, "archimolluscan" configuration included the following characters (as "lowest common denominators") (Fig. 9):

(1) A fairly small body size (2-5 mm) whose ventral surface functioned as a muco-ciliary gliding organ;

(2) a dorsal body surface (mantle) covered with cuticle and unicellularily produced aragonitic, scaly bodies;

(3) the postero-lateral and terminal rims of the mantle delimit and roof an U-shaped groove (rather than a peripedal or purely terminal groove) — the mantle cavity; this is provided with high-prismatic, glandular ephitelium (mucous tracts), with one pair of alternately lamellated ctenidia (without skeletal rods), and with body outlets;

(4) a non-segmented, mesenchymate body cavity including an open haemolymph circulatory system with dorsocaudal heart correlated with the single pair of ctenidia;

(5) three sets of main musculature: (a) a two — or three— layered subintegumental system below the mantle (thus lacking ventrally), (b) a paired submarginal-longitudinal system along the mantle rims enabling the organisms to roll up, and (c) a serial dorsoventral system including two pairs of bundles at each side, the lateral-lower ones intercrossing medially;

(6) a straight alimentary canal including a foregut with a monoserial-distichous radula apparatus for carnivorous nourishment and with associated paired glands; the voluminous midgut lacks separate digestive glands (but has, due to the serial dorsoventral musculature, slight ventrolateral pouches);

(7) paired lateral and ventral medullary nerve cords (amphineurous tetraneury) emerging from a paired cerebral centre and provided with irregular interconnections including a supra-rectal commissure; a simple stomogastric/buccal nervous system;

(8) a terminolaterally innervated, chemoreceptive (osphradial) organ at the midposterior mantle rim (no other distinct sense organs);

(9) a dorsal pair of (gonochoristic?) gonads ontogenetically separated from the mesothelial pericardium. The condition of the primitive gonoducal outlets remains to be clarified: either via the pericardioducts, or by means of proper gonoducts at least functionally separated from the pericardium (in the latter case an original emunctorial function of the pericardioducts also remains to be verified, comp. *p. 17*);

(10) external fertilization with sperm of the primitive type with distal acron and five sphaerical mitochondria; indirect development by means of short-living, lecithotroph Pericalymma larvae (without ocelli, metatroch, or coelom rudiment).

3) *Emergence of molluscan configuration*

Such an original, small-sized organization of Mollusca (the 'archimollusc') was determined by comparatively considering all organ system and their interdependent coexistence (above, items 1-10). This enables the evolutionary emergence of the phylum as well as its anagenetic radiation to be outlined along continuous, functionally combatible pathways.

The acquisition of an alimentary tract with anus (a throughgut) appears to be advantageous as long as organisms remain small (*e.g.* Gastrotricha) and their organs (esp. nervous system and germ cells) receive enough dissolved metabolites (by means of an adjoining midgut filling most of the body as well as through a respiratory and filtering epidermis). Such basically plathelminthomorph, small, slow-moving and probably predacious (*see p. 11*) organisms with anus most probably lived in the aphotic, sublittoral benthos, since molluscs are basically devoid of photoreceptors, and ciliary bottom gliding functions in zones of moderate water movement only. Together with a stabilized body plan (bottom life habit, dorso-ventrality, shape), they developed a dorsal cuticular cover for protection; this differs from general glycocalix secretion (which allows regulative exchange of dissolved organic matter: DOM; *cf.* RIEGER, 1984). This doubtlessly impaired metabolic efficiency locally, a condition counteracted by the enlargement of the (posterio-)lateral body areas free of
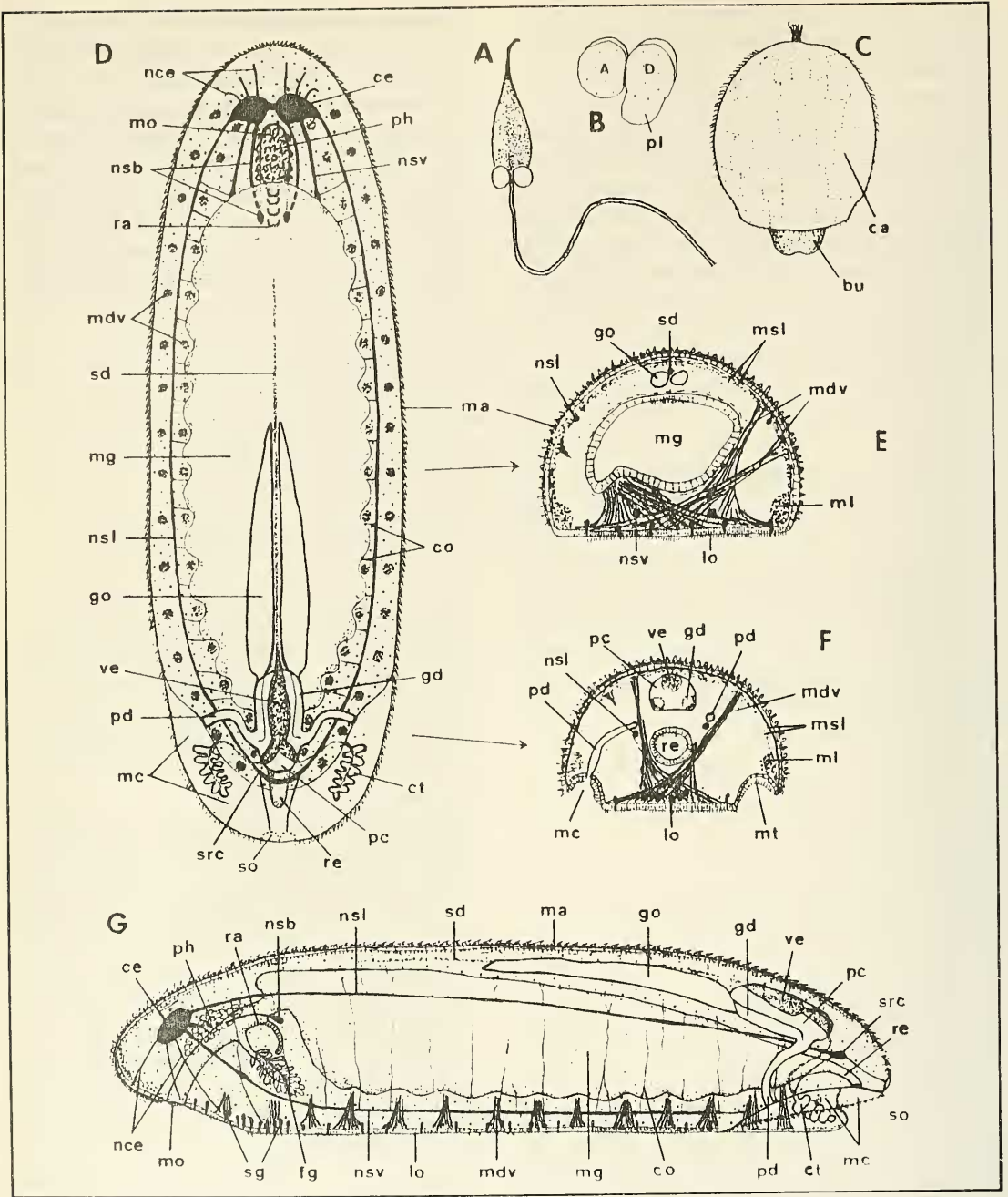
Fig. 9. Most likey organization of molluscan archetype. *A*: Spermatozoon of the so-called primitive type with apical dense tube, distal acrosome and five sphaerical mitochondria; *B*: fourcell stage of cleavage with polar lobe; *C*: Pericalymma larva; *D*: adult organization in dorsal view; *E* & *F*: cross sections as indicated by arrows; *G*: adult organization in lateral view from the left side. (bu = bud of pre-adult organism; ca = calymma (larval test); ce = cerebral ganglion; co = lateroventral connective; ct = ctenidium; fg = ventral foregut gland; gd = gonoducal gutter (ciliary tracts or gonoduct?); go = gonad; lo = muco-ciliary gliding organ; ma = mantle cover of cuticle and scaly bodies; mc = mantle cavity; mdv = dorsoventral musculature; mg = mid-gut; ml = longitudinal (-marginal) muscle; mo = mouth; msi = subintegumental musculature; mt = mucous tract; nce = cerebral nerves; nsb = buccal nervous system; nsl = lateral nerve cord; nsv = ventral nerve cord; pc = pericardium; pd = pericardioduct; ph = pharingeal glands; pl = polar lobe; ra = radula; re = rectum; sd = dorsal blood sinus; sg = sole glands; so = terminal (osphradial) sense organ; src = supra-rectal commissure; ve = heart ventricle).

cuticularization. The simultaneous increasing need for a propulsive organ to circulate the haemolymph for distribution of oxygen and DOM as well as digested food-stuffs favoured the differentiation of a pumping motor. The result was a rudimentary heart which, due to the posterio-lateral rudimentary mantle cavity and its ciliary ventilation, differentiated in the dorso-posterior body region (cf. STASEK, 1972: 8; SALVINI-PLAWEN, 1972: 246, 1981a: 249; WILLMER, 1990: 260). The heart initially most probably consisted of a sinus situated between the dorsal body wall and a ventrally supporting muscular concentration (eventually becoming a vesicle, the pericardium).

The advantage of or even the necessity for circulation of metabolites (be it respiratory oxygen or dissolved foodstuff) is evidenced even in certain small organisms, e.g. higher Kamptozoa (cf. EMSCHERMANN, 1969). This is also true for small animals partly sheltered by a limiting cover (cuticle, shell), e.g. in several veliger larvae (Fig. 10). Such veligers (RAVE , 1958: 154-155; FRETTER & GRAHAM, 1962: 453-454; FIORONI, 1966: 733-734) range from only 0.3 mm to 1.5 mm in size, yet are provided with a larval heart predominantly serving for oxygen circulation. Similar and analogous differentiation of larval hearts in pteropods and terrestrial pulmonates (cf. RAVEN, 1958: 154) demonstrates the functionally and morphogenetically adaptive readiness for a circulation pump.

A more substantial mantle cuticle, pierced by epidermal papillae for minimum contact with the external medium and eventually reinforced by chitin (cf. PETERS, 1972), would have initiated the formation of vascularized dermal protrusion within the rudimentary mantle cavity. These "single pair of complexly folded structures" (STASEK, 1972: 8; SALVINI-PLAWEN, 1972: 313, 1981a: 294, 1985: 133) became the original, alternately lamellated ctenidia. In contrast to YONGE (1947), they were free organs without membranes and skeletal rods (SALVINI-PLAWEN, 1981a: 276-279). Since neither a cuticular cover nor spicule production appear to seriously affect the respiratory capacity of the organisms as a whole (at least as long as ather free epitelia are present; cf. RIEGER & STERRER, 1975; RUNNEGAR & POJETA, 1985: 19-21), the original ctenidia may have predominantly served for ventilation and as osmotic organs for

ionic regulation (esp. ammoniotelic nitrogen metabolism). Only secondarily did they become gills through an increase of the respiratory surface related to body mass (comp. also BROWN et al., 1989). Main excretion may have been realized as in Solenogastres and Caudofoveata (BABA, 1940; HOFFMAN, 1949) via the epidermal papillae and midgut (see also p. 17). The (simultaneously adapted?) secretion of unicellular calcareous bodies by the mantle epithelium may also reflect an excretory process (storage for excess calcium) in addition to contributing to the rigidity and protective function of the mantle cover.

Germ cells presumably were originally embedded within the mesenchyme, as in conservative Turbellaria-Acoelomorpha (cf. HYMAN, 1951: 111). With the fixed function of the heart within a pericardium, the gono-pericardial complex typical for molluscs became established via an association of the gametogonia with the pericardium; this was supplemented by facultative outlets (intercellular rupture) and later on by permanent pericardioducts (= primary gonoducts). It thus originally represented a pericardium with a paired rostral gonocoel and paired gonoducal pericardioducts (cf. HIGLEY & HEATH, 1912; SALVINI-PLAWEN, 1978: 85-95). Such a mere secondary association of the true primordial germ cells with the pericardium ('retroperitoneal' location; cf. HAMMARSTEN & RUNNSTRÖM, 1928: 280; RAVEN, 1958: 254) contradicts the predominantly favoured gonocoel theory for the whole complex (e.g., STASEK, 1972; cf. also WILLMER, 1990: 29-30 & 254).

So-called mucous tracts, composed of slender ciliated cells and hexagonal gland cells, were differentiated in the pallial groove. Their original function is not clear. At least locally correlated with the elaboration of gonopores, these tracts have also auxiliary reproductive function in Caudofoveata (regressive in males), Solenogastres, Ctenidiobranchia ("brood bag" in some female nuculid bivalves), and Siphonopoda (nidamental glands in cephalopods; cf. SALVINI-PLAWEN, 1972: 226-228, 1981a: 279-280). The present dominant function of the mucous tracts (= glandular tracts, hypobranchial glands; Fig. 5) appears to be the adhesive conglomeration of dispersed particles in order to cleanse the respiratory water. In Placophora, the limited extension of the tracts to the

posterior region of the mantle grooves parallels the condition in Caudofoveata as well as Solenogastres (HOFFMAN, 1949; SALVINI-PLAWEN, 1972: 250-253). In addition, there are no indications of lateral or even perioral mantle grooves in Caudofoveata (*cf.* Fig. 7). All these features allow us to infer a purely posterior, U-shaped pallial groove in the original molluscs.

Differentiations within the sensory system started with the concentration of longitudinal nerve fibres into paired ventral cords (see locomotion) and a pair of lateral ones (see mantle rim and postero-lateral pallial groove; internal organs); the result was medullary tetraneury = amphineury

with irregular interconnections. A separate stomogastric (buccal) system was improved with respect to the radular apparatus and the foregut glands. On the other hand, the terminal portion of the lateral cords, interconnected by a supra-rectal commisure, became involved both in the control of ionic regulation/respiration (ctenidia) and in the reception of chemical substances. Perhaps in order to synchronize the release of genital products, this (tentative) function was finally regulated by the chemoreceptive (osphradial), paired terminal sense organ associated with the ventilation at the posterior rim of the mantle groove (*cf.* SALVINI-PLAWEN, 1981a; HASZPRUNAR, 1987a-b). No further
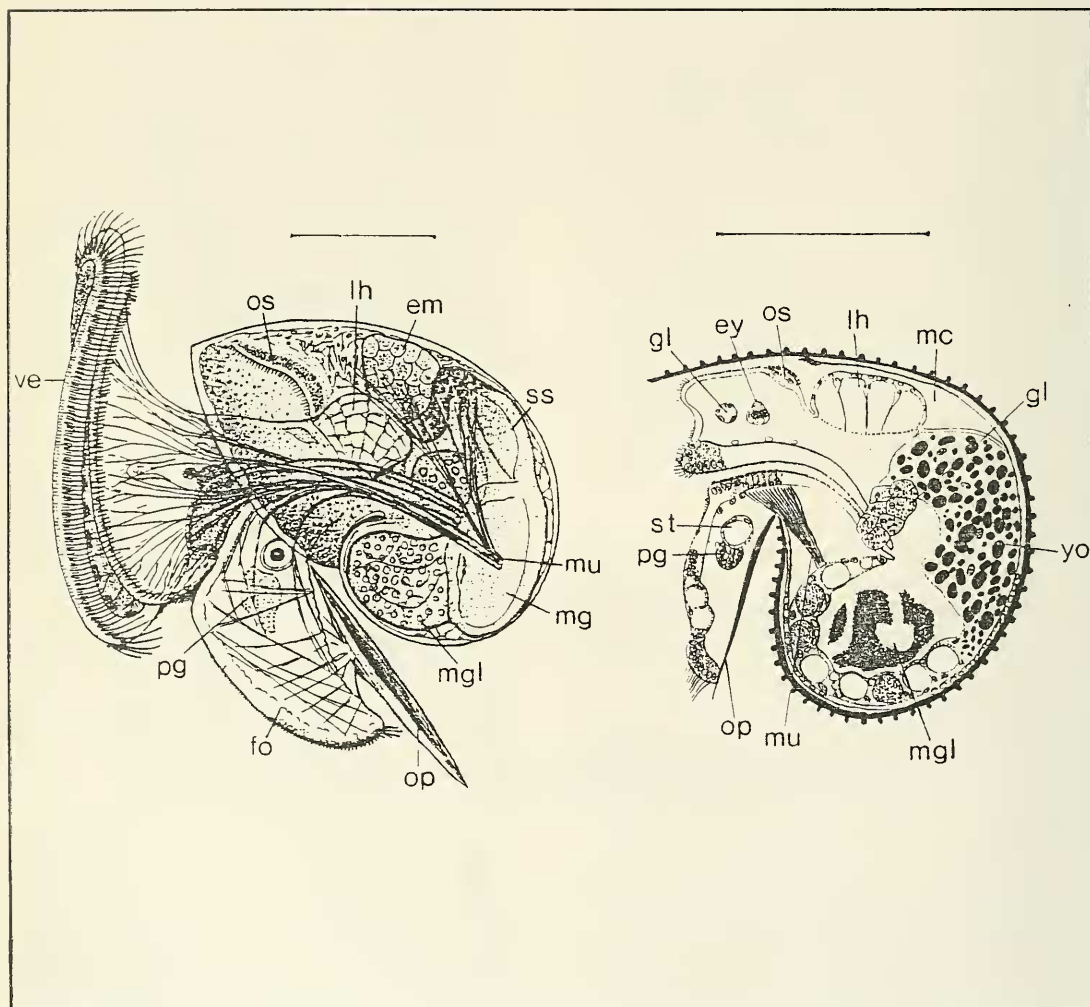

Fig. 10. Planktotrophic Veliger larvae (Caenogastropoda) with larval heart (lh); *Crepidula fornicata* (left; from WERNER, 1955) and *Philibertia purpurea* (sagittal section, right; after FIORONI, 1966). (em = emunctorium; ey = eye; fo = foot; gl = gland cells; lh = larval heart; mc = mantle cavity; mg = stomach; mgl = midgut gland; mu = dorsoventral retractor muscle; op = operculum; os = osphradium; pg = pedal ganglion; ss = style sac of stomach; st = statocyst; ve = velum; yo = yolk; each bar = 100 mm).

distinct sense organ is common to all molluscs.

Along with the above reorganization, the benthic, directed locomotion resulted in elongation of these small organisms. Ventrolateral concentration of longitudinal muscle fibres led to a paired *musculus longitudinalis*; this enabled protective curling and even (in woodlouse fashion) rolling up. It also led to a more distinct seriality of the dorsoventral musculature. The mucociliary gliding was correlated with feeding which, most probably, was carnivorous on sessile, soft-bodies animals (SALVINI-PLAWEN, 1988a: 371). Such nourishment can be inferred from the conditions in the Solenogastres (feeding on Cnidaria). The latter clearly exhibit a most conservative alimentary tract configuration: uniform, sac-like midgut merely showing slight ventrolateral constrictions due to the dorsoventral musculature, and elaboration of a still conservative radula apparatus (*see p. 11*) associated with a pair of foregut glands (*cf.* SALVINI-PLAWEN, 1988a).

No decisive interpretation is possible regarding the excretory system. In contrast to ANDREWS (1985: 386), the pericardioducts of neither the Caudofoveata nor the Solenogastres exhibit emunctorial function (*cf.* also MARTIN, 1983: 361-363): *In vivo* experiments on Solenogastres (BABA, 1940) as well as ultrastructural investigations in Caudofoveata (pers. comm. M. TSCHERKASSKY, Wien) yielded negative results with regard to a cardiac adjustment for ultrafiltration. However, this condition could be secondary since *Phyllomenia* (Solenogastres) possesses proper gonoducts (with retained, modified pericardial outlets) and *Driomenia* (Solenogastres) shows relics of proper gonoducts (*cf.* SALVINI-PLAWEN, 1970). In addition, the Caudofoveata possess a pair of ectodermal, so-called glandular ducts which inter-connect the pericardioducts with the mucous tracts of the mantle cavity. Together with the paired gonopericardial interconnection, these glandular ducts could well represent modified remnants of former gonoducts (*cf.* SALVINI-PLAWEN, 1972: 251-253, 1985: 73) — even if the glandular ducts (rather than the "coelomoducts" = pericardioducts) in some Caudofoveata exhibit an analgous histological similarity with the excretory organ of certain higher molluscs (*Nucula in* SCHELTEMA, 1978: 104). The ontogenetically retarded differentiation of proper gonoducts in Solenogastres (*Phyllome-*

nia; SALVINI-PLAWEN, 1978: 88) and Placophora (HIGLEY & HEATH, 1912) could indeed reflect their convergent, phylogenetically young differentiation. The common ancestors (Fig. 9), then, may have been provided with at least functionally separated, gonoducal gutters or grooves to convey the germ cells through the pericardium into the pericardioducts (= primary gonoducts). True excretory organs, i.e. pericardioducts modified to the Mollusca-specific emunctoria (rather than "nephridia" or "kidneys") cannot be found below the level of Placophora (SALVINI-PLAWEN, 1985: 124). Thus, uncertainly remains as to the level of organization at which[1] the individualization of the gonad from the common gonopericardium and[2] the (polyphyletic?) differentiation of proper gonoducts separate from the pericardioducts (becoming emunctoria) took place (*cf.* also STASEK, 1972: 10). On the other hand, the existence of true emunctoria in Testaria (= Placophora and Conchifera) substitutes the excretory functions of the ctenidia (*see above, p. 15*) and may allow the latter's eventual reduction (*cf.* also RUNNEGAR & POJETA, 1985: 19-21).

4) *Anagenetic differentiation*

The outlined series of partly inter-correlated molluscan characters define the configurations of basically three levels of organization, viz.[1] aplacophoran, [2] polyplacophoran and[3] monoplacophoran (= conchiferan); interconnecting levels can be defined with the Adenopoda and Testaria. Each gave rise to one or more extant clades and thus enables anagenetic differentiation to be traced (Fig. 11).

(1) *The aplacophoran level*: This level of organization includes the outlined common archetype of molluscs as well as the conservative extant Caudofoveata and Solenogastres. Both the latter have retained the aculiferan mantle cover (cuticle, aragonitic bodies; *cf.* SALVINI-PLAWEN, 1990a) and the straight gut. The gonads of both also shed their products via a pair of short ducts through the pericardium and pericardioducts to the exterior; this condition may either be plesiomorphic (?) or convergently secondary (see above, p. 17).

The evolutionary pathway towards the *Caudofoveata* is basically dominated by the change in life habit from muco-ciliary gliding to burrowing in

sediment. This development, probably coinciding with preferred nourishment on infaunal organisms, led to a new main orientation of the body along the anterior-posterior axis (in contrast to the dorso-ventral relation). The result was a lateral rounding off and an elongate, worm-like shape. This also involved reduction of the main locomotory surfa-
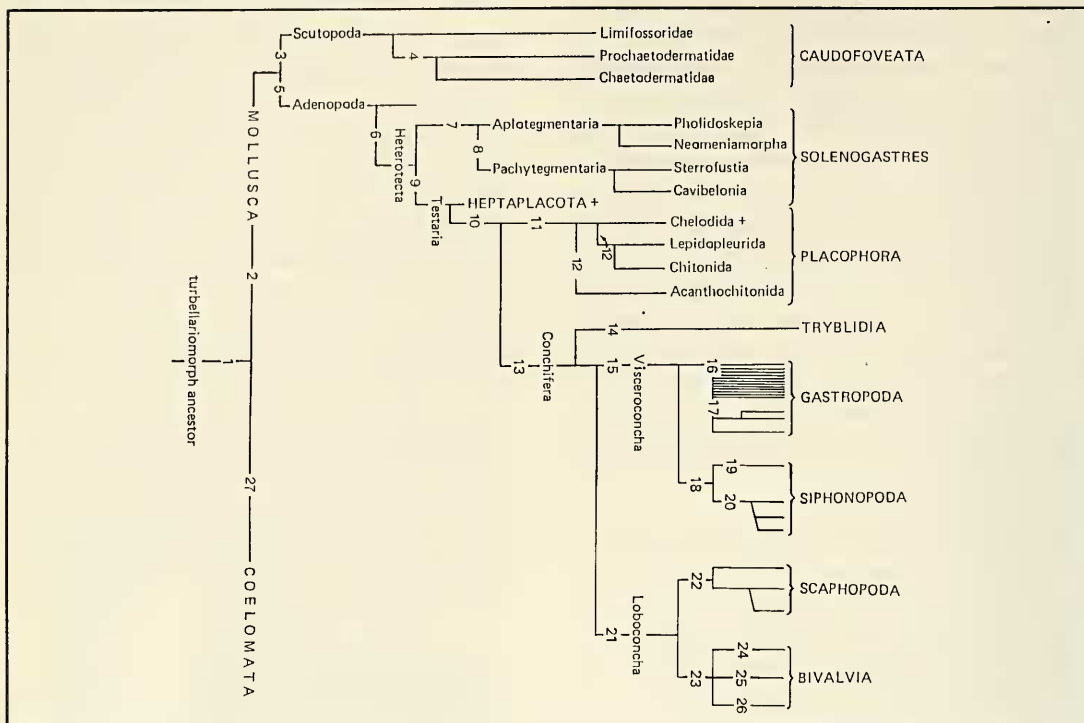

Fig. 11. Relationship and classification of Mollusca (based on SALVINI-PLAWEN, 1985 and 1990a).[1] Mesenchymate, muco-ciliary gliding Spiralia, with Pericalymma larva;[2] molluscan archetype with mantle cover, radula, etc. (see pp. 12-13 and Fig. 6);[3] infaunal burrowing habits resulting in wormshaped body and respective reorganization: Caudofoveata;[4] radular ribbon reinforced below each pair of teeth;[5] mantle cavity preorally united, locomotion restricted to ventrally-innervated section (foot) with pedo-frontal gland: Adenopoda;[6] arrangement of middorsal mantle bodies in seven transverse rows of juxtaposed elements: Heterotecta;[7] Cnidaria-vory with narrowing of body as well as foot, and with respective reorganization: Solenogastres;[8] thick cuticle with stalked mantle papillae, spicules multi-layered;[9] fusion of middorsal transverse rows of scaly bodies to form shell-plates/valves with inclusion of mantle papillae: Testaria;[10] subradular organ, reorganization of midgut, differentiation of emunctoria and aorta;[11] multiplying of ctenidia, radula with 17 teeth per row, photoreceptive aesthetes, larval ocelli: Placophora;[12] differentiation of articulamentum;[13] homogeneus shell-gland producing concha, free head with appendages, jaw formation, stomach with protostyle, statocysts: Conchifera;[14] metabolic and circulatory reorganization (repetition of ctenidia and of heart-auricles, subdivision of emunctoria): Tryblidia;[15] head with cerebral photoreceptors, restriction of mantle and shell to the visceral body and mantle cavity to the posterior, lateral nerve cords medial of dorsoventral musculature: Visceroconcha;[16] torsion of visceral complex with streptoneury, reduction of original right gonad, one pair of dorsoventral muscles, shell operculum: Gastropoda-Streptoneura with at least 12 offshoots (compare at last HASZPRUNAR, 1988);[17] parietal ganglia, subcerebral commissure, plicatidium, repugnatorial glands, hermaphroditism: Pentaganglionata = Euthyneura (see Fig. 14);[18] septate concha transversed by mantle sipho (siphuncle), head appendages becoming grasping arms, foot altered to funnel/siphon; Siphonopoda ("cefalopods");[19] multiplying of arms, repetition of ctenidia, subdivision of emunctoria: Nautiloida;[20] restriction of radula (9-5 teeth per row) and differentiation if ink sac, both which also refer to Ammonoida; mantle covers shell with successive regression of shell, differentiation of branchial hearts: recent Coleoida with radiation into Decabranchia, Vampyromorpha, and Octobranchia;[21] lateral enlargement of mantle and concha, anterior elongation of foot: Loboconcha;[22] ventral fusion of mantle lobes, reduction of ctenidia, head appendages becoming captacula: Scaphopoda (cf. Fig. 13);[23] suppression of calcification along middorsal longitudinal line of shell, suspension-feeding with reduction of buccal region: Bivalvia with three recent clades;[24] deposit-feeding, head appendages (labial flaps) with tentaculated palp: Ctenidiobranchia/Nuculida;[25] filter-feeding by means of the foliated (= plain-faced) ctenidia: Palaeobranchia/Solemyida;[26] filter-feeding by means of the axially elongated ctenidia with multiplied elongated lamellae, paedomorphy of byssus gland, differentiation of protonephridia: Autobranchia (with filibranch, lamellibranch and septibranch subgroups);[27] infaunal-burrowing locomotion with microvory inducing vermiform body and ventral ciliation, differentiation of secondary body cavity with coelomate organization: Coelomata.

ce, midventral fusion of the lateral mantle rims, shift of the pallial groove to the terminal end of the body with inversion of its organs (ctenidia, mucous tracts; see Fig. 5), and reinforcement of the longitudinal layer of the subintegumental musculature at the expense of the dorsoventral system. A postoral area of structurally particular body epithelium functioned as a digging locomotory organ facilitating burrowing (hence: pedal shield, oral shield; *see p. 9*). The microvorous nourishment also influenced the alimentary canal and favoured the specialization of the posterior midgut to be splitted into intestine and large midgut sac (*see above p. 11*, and SALVINI-PLAWEN, 1981b, 1988a).

In contrast, the forerunners of the hermaphroditic *Solenogastres* retained their epibenthic habits. The result was an anterior elongation and preoral merger of the mantle groove. In addition, a distinct pedal gland at the anterior border of the ventrally-innervated portion of the gliding sole was formed. The presence of this pedal gland defines the recent Solenogastres and Placophora as well as Conchifera within a common level of ADENOPODA, in contrast to Caudofoveata = SCUTOPODA (*see p. 10* and SALVINI-PLAWEN, 1972: 294-309, 1981a, 1985). Moreover, devolepmental particularities (*cf*. PRUVOT, 1890) suggest common precursors of Solenogastres and Placophora whose mid-dorsal mantle spicules were arranged into seven successive rows of adjacent scaly bodies; these were set off from the disordered scales of the flanks (Fig. 5 br). This elaboration was later lost in the Solenogastres proper, which fed on Cnidaria and successively adapted a winding-wriggling locomotion (secondary hard bottoms with hydroids, coral colonies; *cf*. SALVINI-PLAWEN, 1981b).The result was a simple narrowing of the body and the foot, as well as regression of the antero-lateral pallial cavity and an internalization of the latero-posterior portions of the mantle groove. They became the actual mucous spawning ducts (Figs. 5 & 7) into which the pericardioducts open; the ctenidia were reduced, although ventilation is maintained by other ciliated epithelial surfaces in mantle cavity.

(2) *The polyplacophoran level:* The trend to reinforce the mantle cover, probably associated with the advancement into tidal zones of hard bottoms, led to the polyplacophoran level and to the origin of the clade Testaria (= Placophora plus Conchifera). The consolidation of the juxtapo-

sedly secreted scales into seven rows (above) to form seven imbricating plates (SALVINI-PLAWEN, 1985: 113-114) is supported by developmental patterns (KOWALEVSKY, 1883a; MINICHEV & SIREKO, 1984; *cf*. Fig. 5). This initial configuration as well as the frequent abnormality of predominantly seven valves only in recent forms (TAKI, 1932; LANGER, 1978; DELL'ANGELO, 1982) suggest seven-plated forms or *Heptaplacota* as immediate forerunners of the extant representatives, regardless of whether the known records of fossil *Septemchiton*-species are valid (*cf*. SALVINI-PLAWEN, 1981a: 258-259; ROLFE, 1981). Later on an eighth valve or plate was added, leading to the loricate *Placophora*; the serial pairs of dorsoventral muscle bundles became arranged accordingly (two pairs per plate). Mantle papillae enclosed within the plates became elaborated for negative phototaxis (aesthetes; *cf*. FISCHER, 1978). The more complex digestive conditions (feeding by scraping algae) favoured the elaboration of the gut: operation of the radular apparatus (stereoglossate condition; *cf*. SALVINI-PLAWEN, 1985: 359-360), well-defined foregut glands and subdivision of the midgut into a distinct oesophagus with lateral pouches, stomach with laterally differentiated digestive glandular organs and somewhat looped intestine (*cf*. Fig. 8). In addition, a chemoreceptive sense organ within the eversible subradular pouch enabled examination of food before uptake. This differentiation and the adhesion to hard substrates in the upper sublittoral zone led to the adaptation or more specialized elaboration of the excretory functions of the heart (ultrafiltration) and pericardioducts (emunctoria); it also initiated the compensatory multiplication of the ctenidia for respiration.

(3) *The monoplacophoran level*: The emergence of the monoplacophoran level was most probably realized by the fusion of the eight formative areas of placophoran plates to a concha-producing shell-gland (*cf*. HAAS, 1981). This is supported (1) by the fossil *Merisconchia* (Fig. 12) which show the first and the second valves (with a pair of muscle scars) still separated from the remaining shell (with six pairs of muscle scars) by distinct furrows (*cf*. YU, 1984, 1987); (2) by the arrangement of the dorsoventral musculature in recent Tryblidia (*cf*. HAAS, 1981; SALVINI-PLAWEN, 1981a: 242-244; also WINGSTRAND, 1985); (3) by the existence of

shell-perforating mantle-papillae in various Con-hifera (similar to the enclosed aesthetes; *cf.* SALVI-NI-PLAWEN, 1985: 115-116). A prerequisite for such a fusion process would have been the loss of the necessity for the animals to roll up (the *musculus longitudinalis* shifting to a pedal position, *cf.* Fig. 5), possibly due to a fairly adhesive existence. Correlatedly, perioral/labial (head) appendages were differentiated for microvorous feeding; this was supplemented by cuticularization in the pharynx (jaw formation; *cf.* SALVINI-PLAWEN, 1985, 1988a). The digestion of such food implied the subsequent elaboration of the specialized pro-tostyle-sac type of stomach (*cf.* Fig. 8 and SALVI-NI-PLAWEN, 1988a: 366-370).

Such a monoplacophoran organization, comple-mented by statocysts and a sub-rectal commissure, is basic to all (at least extant) Conchifera. Recent *Tryblidia* have largely retained this configuration, but have adapted certain additional characters

geared to metabolic requirements: the more effi-cient and interdependent elaboration (and subdivi-sion) of the emunctoria, the ctenidia, and bran-chio-auricular connections (*cf.* SALVINI-PLAWEN, 1988b). Other, fossil conchiferan lines probably also diverged from such primitive level, especially those subsumed under the paraphyletic "Galero-concha" or "Monoplacophora" (*cf.* SALVINI-PLAWEN, 1980, 1981a; POJETA & RUNNEGAR, 1976; RUNNEGAR & POJETA 1985: 25-32; YU, 1987).

Extant representatives subsequently diverged into two clades: (a) Organisms penetrating soft bottoms adapted an anterior elongated foot and a laterally enlarged mantle with shell to envelop the entire body. Such *Loboconcha* (= Diasoma, Ancy-ropoda) include the fossil Rostroconchia and the Bivalvia as well as Scaphopoda, which are ob-viously derived from the former. Deposited and/or
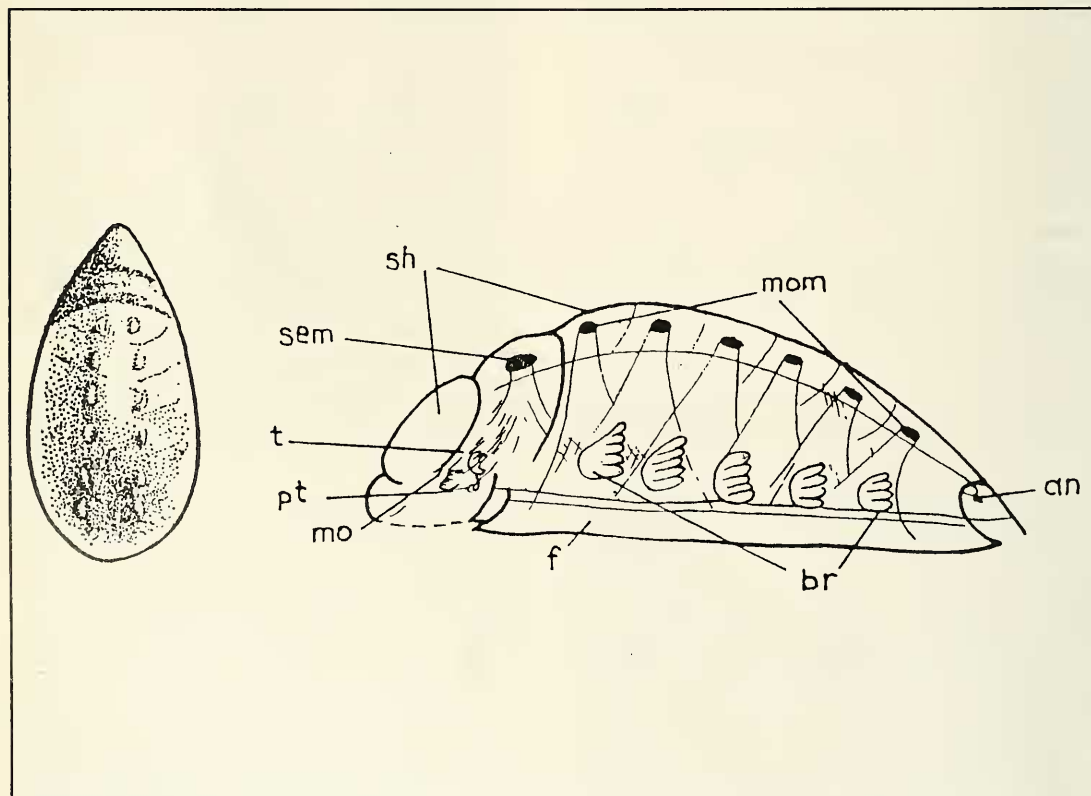

Fig. 12. MERISMOCONCHIA, dorsal view with muscle scars (left) and reconstructed organization (after YU, 1984). (an = anus; br = ctenidia; f = foot; mo = mouth; mom = dorsoventral muscle bundles III-VIII; pt = postoral tentacle; sem = muscle bundle II; sh = shell; t = preoral tentacle).

suspended food led to the adaptation of the perioral/labial appendages or to mucociliar palp-feeding. This paralleled the regression of the buccal apparatus (but not the "head" with cerebral ganglia). The thus emerged *Bivalvia* (*cf.* SALVINI-PLAWEN, 1980a: 262-263; 1981a: 268-270) radiated according to different feeding strategies along three adaptive lines (Ctenidiobranchia, Palaeobranchia, Autobranchia). Only one, the lamellibranch Autobranchia, were quantitatively successful. Other Loboconcha became true infaunal species which searched for small prey (micro-carnivory) by means of specialised head appendages (captacula); this infaunal habit favoured the midventral fusion of the mantle and shell as it is in *Scaphopoda* (*cf.* SALVINI-PLAWEN, 1981a: 271-272, 1988a: 343-344).

b) The second clade improved the plantigrade locomotion and differentiated a free head with cerebral photoreceptors. This restricted the mantle and shell to the increasingly conical visceral body and limited the mantle groove to a mere posterior cavity. These *Visceroconcha* (= Rhacopoda; not identical, however, with the "Cyrtosoma" of RUNNEGAR & POJETA, 1985: 25, which include the "Monoplacophora") also share the lateral/pleural nerve cords medial to the dorso-ventral musculature; moreorer, they are provided with an antogonistic, three-dimensional muscle-on-muscle system (*see above, p. 12*). Within that frame, the *Gastropoda* are characterized by the particular event involving two-phased torsion: the first phase was probably advantageous for equilibrium problems of early lecitrotroph larva, the second one merely represents regulative differential growth (*cf.* SALVINI-PLAWEN, 1981a: 261-263; HASZPRUNAR, 1988: 405-407). As a probable consequence of torsion, the pretorsional right reproductive system became reduced and an operculum was adapted. On the other hand, hypertrophy of orthoconic or slightly cyrtoconic shells might well have led to a septate condition — as in certain gastropods and extinct groups. The apical mantle area in one such groups, however, retained permanent connection with the concha and thus formed a mantletube or siphuncle. This mantle/shell configuration appears to have been the prerequisite for the differentiation of *Siphonopoda* = cephalopods (SALVINI-PLAWEN, 1981a: 265-267). The permeable siphuncle enabled the extraction of chamber-liquid and partial replacement with gas for buoyancy (*cf.* SALVINI-PLAWEN, 1981a: 265-266; TEICHERT, 1988: 67-69). The differentiation of parapodia-like enlargements of the foot allowed a floating-fluttering mobility (later rolled and meeting or merging ventrally to form the funnel for jet propulsion). The perioral/head tentacles grasped small organisms (omnivory to necrophagy); later, these cerebrally-innervated (!) tentacles (YOUNG, 1977, 1988; SALVINI-PLAWEN, 1980a, 1981a) became elaborated into several (already ten?) modified organs (again multiplied in the nautiloid line). The foot with pedal gland is merely represented by the funnel or siphon with funnel gland (hence: 'siphono'-pods, rather than "cephalo"-pods).

CLASSIFICATION

Classification should represent the natural system and evolutionary pathways. The anagenetic differentiation of the Mollusca outlined above must be incorporated into modern classification schemes. The following critical appraisal should be helpful in such a compiled systematic survey.

1) General remarks

(a) The long-standing classification of Caudofoveata (= animals with terminal (pallial-)cavity) and Solenogastres (= animals with a mid-ventral channel or (pedal) groove) within one class "Aplacophora" is untenable. As outlined above (*p. 18, 19*), the configuration of the mantle cavity in each group (Fig. 5) demonstrates that two different processes are responsible for the vermiform or slender shape of the Caudofoveata and the Solenogastres. This clearly contradicts a derivation of one from the other (SALVINI-PLAWEN, 1985, 1990b). Both the lateroventral inversion in Caudofoveata (*p. 18*) and the simple lateral narrowing in Solenogastres (*p. 19*) represent para-phyletic conditions. They can be interrelated only if traced back to and originating from broad, ciliarily-gliding organisms (Fig. 5 A). In addition, neither group possesses a single commonly-derived (synapomorphic) character which would demonstrate a closer relationship other than in a common archimolluscan ancestry (plesiomorphies). This also refers to the gonopericardial complex (*p. 13/15*); it supports the argument that the lack of true gonoducts is analogous (due to narrowing of the bodies). Thus, at least the conditions of the mantle cavities (rather

than because of the pedal condition, *see p. 10* and the mis-interpretation by SCHELTEMA, 1978 and 1988: 61), Caudofoveata (Chaetodermomorpha) and Solenogastres (Neomeniomorpha) represent two separate, paraphyletic clades. These qualitative differences, irrespective of the diverging numbers of species, requires classification as separate classes.

(b) A similar condition involves the two paraphyletic bivalve subclasses Ctenidiobranchia (Nuculida, Ctenodonta) and Paleobranchia (Solemyida, Cryptodonta), generally united under a single taxon "Protobranchia" (*cf.* SALVINI-PLAWEN, 1980: 262-263, 1981a: 269-270; ALLEN, 1985: 349).

(c) The term "Amphineura", formerly used to include Polyplacophora and Aplacophora (above) within one subphylum (alongside the subphylum Conchifera), is misleading and out-of-date: amphineury is retained in Placophora and Tryblidia only. Aculifera is the more appropriate term for the lower Mollusca to contrats them to Conchifera.

(d) Among Scaphopoda (Fig. 13), the order Gadilida (= Siphonodentaliida) embraces two distinct levels (suborders), the Entalimorpha and Gadilimorpha (STEINER, 1990).

(e) The large number of fossil Siphonopoda generally subsumed under Nautiloidea is more appropriately subdivided into the basic stock of Orthoceratoida (=Palcephalopoda when including the Actinocerida and Endocerida) and Nautiloida s.str. (*cf.* SALVINI-PLAWEN, 1980a: 265-266, 1981a: 267-268; TEICHERT, 1985: 19-21).

(f) The familiar three divisions of the Gastropoda into "Prosobranchia", Opistobranchia and Pulmonata is no longer satisfactory. More recent investigations demonstrate that the nervous system is more reliable with respect to high level organisation. The subclades should therefore preferably be termed 'Streptoneura' and 'Euthyneura'. Herein, the Steptoneura are thoroughly reclassified according to synapomorphic characters as discussed in SALVINI-PLAWEN & HASZPRUNAR (1987) and summarised in HASZPRUNAR (1988).

— The Euthyneura (Fig. 15) basically share the pentaganglionate visceral system (i.e. with parietal ganglia), a second (= delicate sub-) cerebral commissure, as well as repugnatorial glands (tectibranch *Acteon, Hydatina, Ringicula*, and some Bullomorpha; gymnomorph *Onchidella* and *Veronicella*; lower pulmonate *Siphonaria* and Ellobiidae). In addition, they have a plicatid gill in common, newly established at the site of the former left ctenidium. This plicatidium is therefore not homologous to the prosobranch gill (*cf.* HASZPRUNAR, 1985, *versus* SCHMEKEL, 1985); the terms "Euctenidiacea/Ctenidiacea", "Actenidiacea" and "Pseudoeuctenidiacea" (TARDY, 1970; SCHMEKEL & PORTMANN, 1982; SCHMEKEL, 1985; WÄGELE, 1989) used to classify anthobranch and nudibranch gastropods are thus at least ambiguous or even clear misnomers. The Euthyneura include the Opisthobranchia, the Gymnomorpha and the Pulmonata (see below).

— The Opisthobranchia differentiated the head-shield and the paired, so-called Organ of Hancock between head-shield and foot. The monophyly of all opisthobranch groups is evidenced by the common outer branch of the labio-tentacularis nerves (not existent in Gymnomorpha and Pulmonata); this paired nerve is a true synapomorphic character (see HASZPRUNAR, 1988: 422-426, for our need for clear synapomorphies) and provides either the anterior portion on Hancock's organ or the anterior/frontal/oral tentacles (or the rudiments thereof; *cf.* HUBER, 1987). The other portion of Hancock's organ is innervated by the paired rhinophoral nerves, already differentiated in Pyramidellidae. In Anaspidea, Acochlidio-morpha, Gymnosomata and Eleutherobranchia the rhinophoral nerves supply the (true) rhinophores. In the Saccoglossa* without head-shield, however, they innervate together with the head-shield nerves (nn. clypeo-capitis = nn. tentacularis of Streptoneura and neotene Thecosomata), the single or bifid/bifurcate (posterior) head appendages; these latter are consequently not homologous with the rhinophores but with the posterior head-shield areas *plus* Hancock's organ, and should thus be termed 'rhinotentacles'. On the other hand, Eleutherobranchia as well as the small-sized Acochlidiomorpha, Rhodopemorpha and *Philinoglossa* have regres-

---

* [1] from Greek *sakkos* = sac or sack (Greek *sakos* is inaccurate, since this refers to a "large shield") and latinized to *saccus* (not *sacus*); Greek *glossus* (ex *glota*) = tongue. Consequently, the argumentation by Marcus (1982: 10) in favour for Ascoglossa fails, since Saccoglossa is not a compound (Latin and Greek)name.

sed both the head-shield and its clypeo-capitis (= tentacle) nerves.

—The relationships among Tectibranchia remain ambiguous due to the lack of known synapomorphies. Whereas the Ringiculoidea and Acteonoidea undoubtedly represent the most conservative stock (Architectibranchia), only the (anterior) gizzard appears to mark a true synapomorphy at least for Bullomorpha, Anaspidea and Thecosomata (Paratectibranchia, SALVINI-PLAWEN, 1988a:

326, emend.). This anterior gizzard is also present in Umbraculomorpha. In Thecosomata, most probably paedomorphy/neoteny occured at the second larval stage after BROWN (1934) which implied the loss of the head-shield and Hancock's organs (as well as the respective innervation) and the retension of heterostrophic shell as well as of the gizzard. The lack of gizzard in Saccoglossa and Acochlidiomorpha may be primary, as is the case
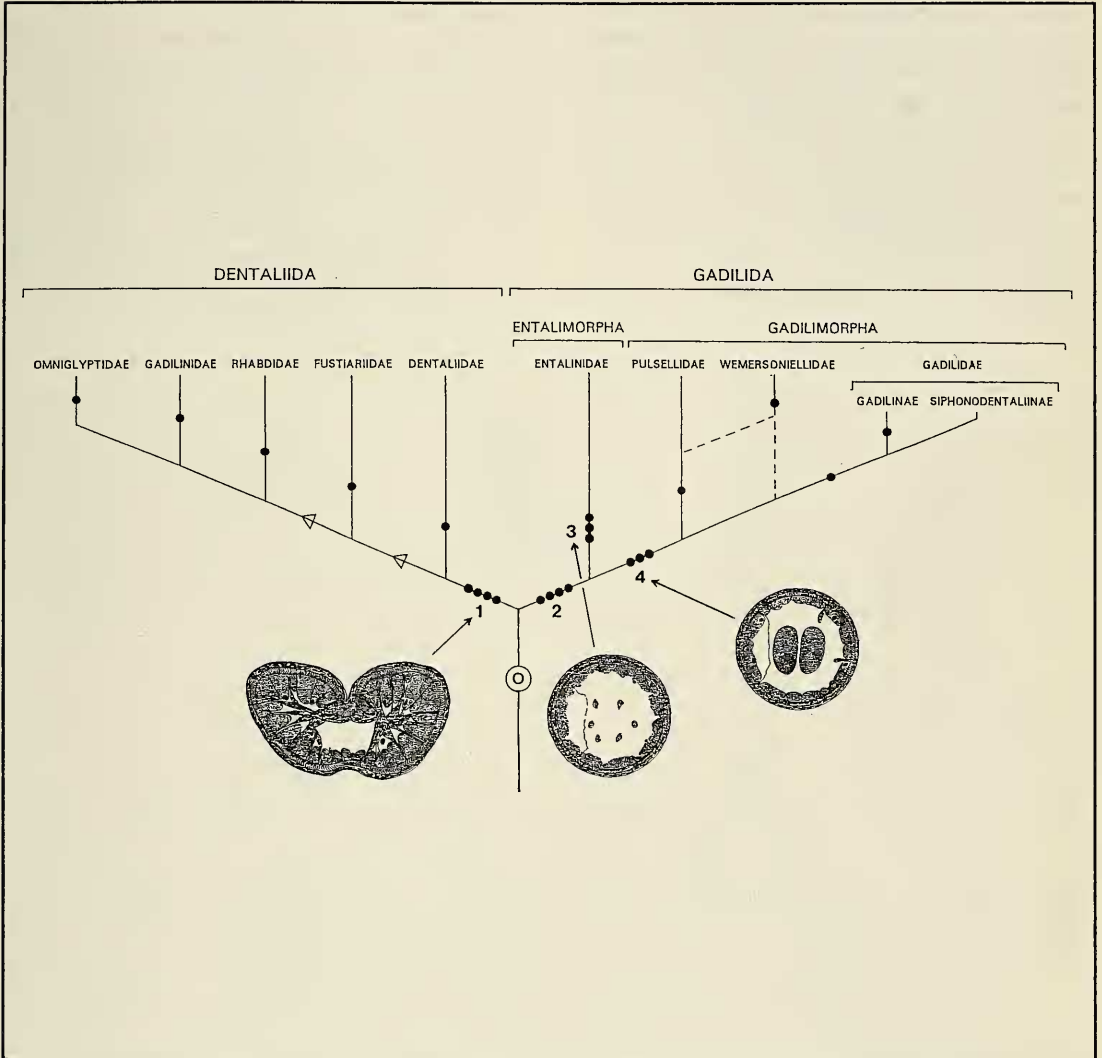

Fig. 13. Phylogenetic reconstruction of pathways in Scaphopoda (combined after STEINER, 1990).[0] = Common scaphopod ancestor;[1] = Dentaliida: foot with distal epipodial-lobes for anchorage and strong peripheral muscle bundles only (inset), two pairs of dorsoventral body retractors, captacula with 10 retractors, central radula teeth wider than tall; [2] = Gadilida: foot with distal pedal disk and separated central retractors, one pair of dorsoventral body retractors, captacula with 7-5 retractors, central radula teeth taller than wide; [3] = Entalimorpha: foot with 4-6 central retractors (inset), lateral teeth of radula with 5-9 denticles;[4] = Gadilimorpha: foot with two central retractros (inset), lateral teeth of radula with three prominent denticles, marginal teeth with keel.

in the cephalaspidean Architectibranchia and Diaphanoidea: On one hand, the genus *Cylindrobulla* is intermediated between Diaphanidae and Saccoglossa based on its radula (*cf.* GASCOIGNE & SARTORY, 1974: 122; THOMPSON, 1979: 340; MARCUS, 1982: 10-12). On the other hand, the radulae of Acochlidiomorpha parallel certain Diaphanidae as well as Saccoglossa (Fig. 14; *cf.* also ODHNER, 1937). As far as known, members of both Diaphanidae *(Diaphana minuta)* and Acochlidiomorpha *(Hedylopsis suecica, Pontohedyle milaschewitchii)* are micro-omnivorous to micro-herbivorous (JAECKEL 1952, Hadl et al. 1970). Diaphanoidea, Saccoglossa, and Acochlidiomorpha may thus be suggested to represent an interrelated stock with mosaic evolution: Dystectibranchia nov. The aberrant, a-tectibranch Rhodopemorpha including *Helminthope psammobionta* and five presumed species of *Rhodope* likewise belong to the Tectibranchia (*cf.* SALVINI-PLAWEN, 1987, 1990c; also

HUBER, 1987; HASZPRUNAR & HUBER, 1990). They share with Acochlidiomorpha calcareous, subepidermal spicule formations (*cf.* RIEGER & STERRER, 1975), which could indicate closer affinities (both Rhodopidae and Hedylopsidae also show monaulic genital system; *cf.* ODHNER, 1937); however, this character could also be due to the predominantly interstitial habitat.

— Relationships among Eleutherobranchia appear to be indicated by several synapomorphies in anagenetic arrangement (Fig. 15). The restriction of the right digestive gland into a caecum or its loss altogether was used by WÄGELE (1989) as a synapomorphy for Anthobranchia and *Doridoxa*. This loses that particular phylogenetic weight due to similar conditions in Bullomorpha (*Philinoglossa*), Rhodopemorpha (*Rhodope*), or Nudibranchia-Arminiacea (*Marionia*). The independent lines of Umbraculomorpha (SCHMEKEL, 1985) and Pleurobranchia (IHERING, 1922) are confir-
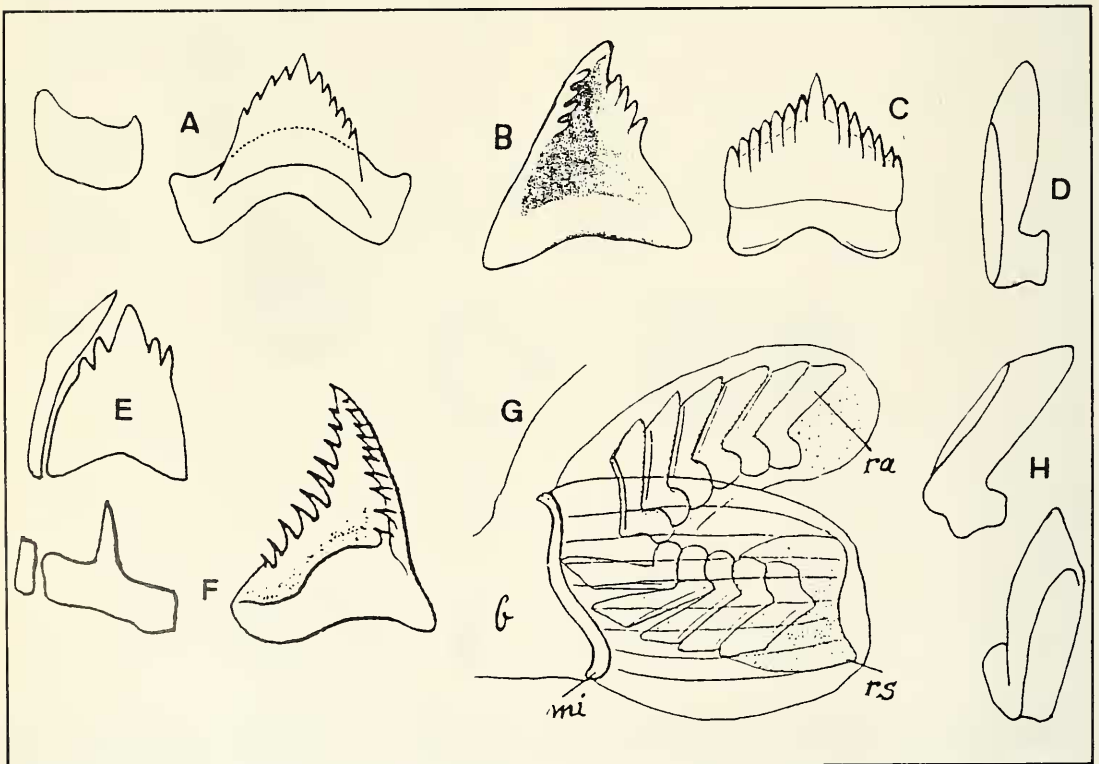

Fig. 14. Radula teeth of Dystectibranchia: A-B = Diaphanidae; C-D = Saccoglossa; E-H = Acochlidiomorpha. A *Toledonia major* (Hedley), B *Newnesia antarctica* Smith, C *Cylindobulla beaui* Fischer, D *Placida dendritica* (Alder & Hancock), E *Unela remanei* Marcus, F *Acochlidium weberi* (Bergh), G & H *Ganitus evelinae* Marcus (G whole radula from lateral, H two teeth). (b = buccal cavity; mi = mandible; ra = radula teeth; rs = radula support). (after HOFFMANN, 1938; MARCUS, 1953, 1982; GASCOIGNE & SARTORY, 1974).

med, and the Nudibranchia (s.str. = Cladohepatica) are well-separated from Anthobranchia (= Holohepatica) and Doridoxamorpha (nov., pro "Pseudoeuctenidiacea" TARDY).

— The Gymnomorpha (Onchidiida and Soleolifera) are characterized by the restriction of the mantle cavity to a mere cloaca (cf. SARASIN & SARASIN, 1899; FRETTER, 1943) and by the differen-

tiation of non-homologous, secondary respiratory organs. These are the so-called ureter gland in Solcolifera and a pulmoary space in Onchidiida (incorrectly cited by HASZPRUNAR & HUBER, 1990: 186; pers. comm. B. RUTHENSTEINER). In addition, the retained prosobranch tentacles are supplemented by the eyes, and the genital system is diaulic (in some onchidiids the closed vas deferens
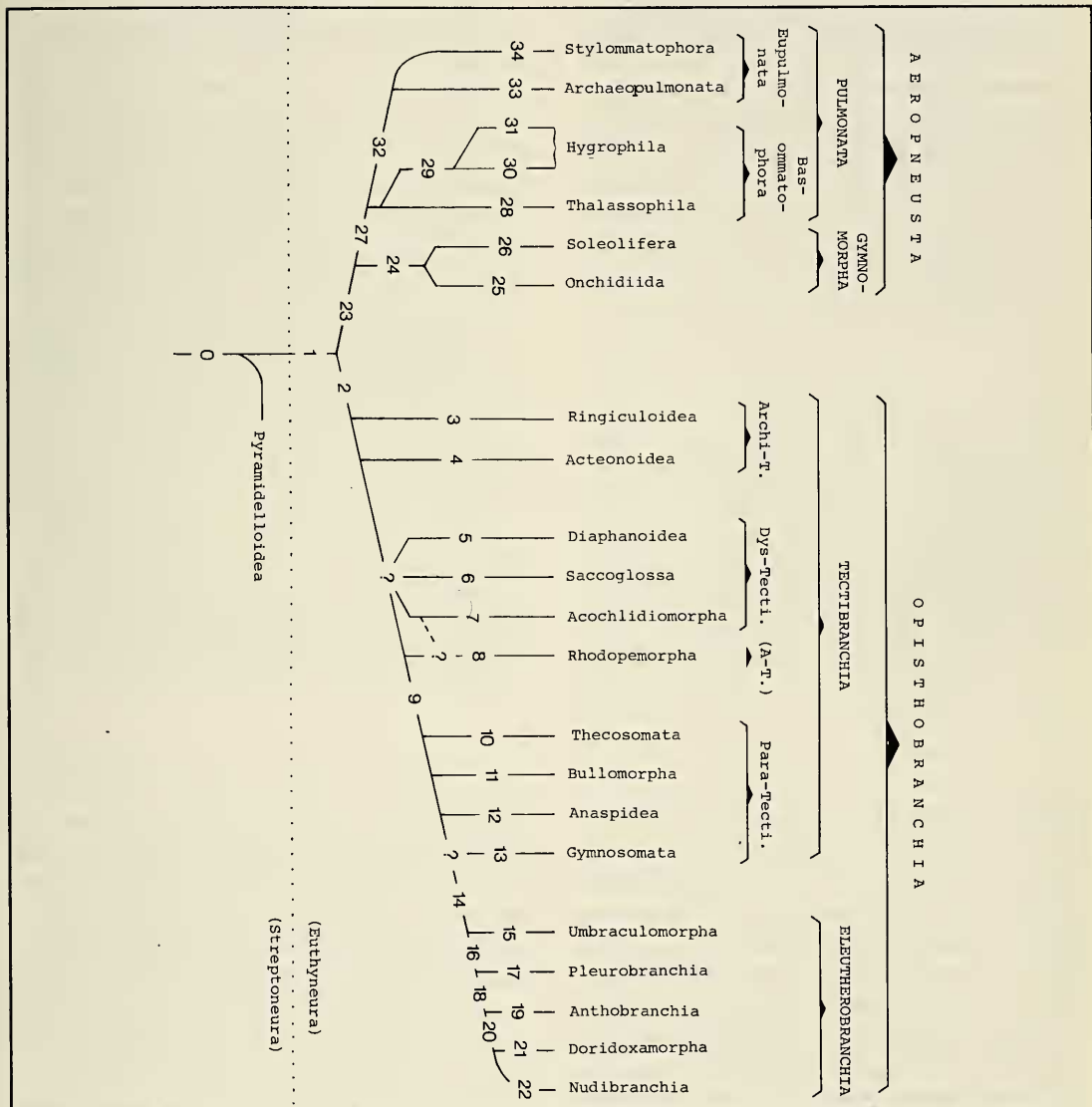
Figure 15 (phylogenetic cladogram). Terminal taxa and associated node numbers, with higher-group brackets:

- 34 — Stylommatophora
- 33 — Archaeopulmonata   } Eupulmonata
- 31, 30 — Hygrophila
- 28 — Thalassophila   } Basommatophora
- 26 — Soleolifera
- 25 — Onchidiida   } GYMNOMORPHA
- (Eupulmonata + Basommatophora = PULMONATA)
- (PULMONATA + GYMNOMORPHA = AEROPNEUSTA)
- 3 — Ringiculoidea
- 4 — Acteonoidea   } Archi-T.
- 5 — Diaphanoidea
- 6 — Saccoglossa
- 7 — Acochlidiomorpha   } Dys-Tecti. (A-T.)
- 8 — Rhodopemorpha
- 10 — Thecosomata
- 11 — Bullomorpha
- 12 — Anaspidea
- 13 — Gymnosomata   } Para-Tecti.
- (Archi-T. + Dys-Tecti. + Para-Tecti. = TECTIBRANCHIA)
- 15 — Umbraculomorpha
- 17 — Pleurobranchia
- 19 — Anthobranchia
- 21 — Doridoxamorpha
- 22 — Nudibranchia   } ELEUTHEROBRANCHIA
- (TECTIBRANCHIA + ELEUTHEROBRANCHIA = OPISTHOBRANCHIA)

Node numbers: 0, 1, 2, 23, 24, 27, 29, 32, 9, 14, 16, 18, 20.

Left-side labels: Pyramidelloidea; (Streptoneura); (Euthyneura).

Fig. 15. Phylogenetic reconstruction of pathways in recent Gastropoda-Euthyneura (compare also pp. 22):[0] = Streptoneura with (Apogastropoda) epiathroid nervous system, bifurcated tentacle nerves and parapedal commissure; with (Allogastropoda) heterostrophy, two opposed ciliated tracts in the mantle cavity devoid of ctenidia; eggs united by chalazae, sperm of spiral type with glycogen helices within midpiece. Newly differentiated (cerebral-)rhinophoral and (pedal-)lateral nerves.[1] = EUTHYNEURA: Elongation of head-pedal complex with parietal ganglia, with subcerebral commissure, pallial caecum, plicatid gill (= plicatidium), and repugnatorial glands; hermaphroditic and monaulic genital system with pallial gonoduct, open seminal groove, bursa copulatrix (distal) and receptaculum seminis (proxi-

mal); chromosomes: n = 16.[2] = OPISTHOBRANCHIA: Burrowing habits with head-shield with incorporation of bifurcated tentacle = clypeo-capitis nerves; rhinophoral nerves provide new Hancock's sense organs with newly differentiated external branch of labiotentacularis nerves for their anterio area; with giant nerve cells; chromosomes: n = 17.[3] = Head-shield and parapodia form median siphon; protrusible cephalic penis.[4] = Fusion of pleural with cerebral ganglia; androdiaulic genital system with closed vas deferens.[5] = Anterior portion of both head-shield and foot with tentaculiform enlargements, radula with prominent (Diaphanidae) or without central tooth (Notodiaphanidae).[6] = Monostichogloss radula with saccus; fusion of cerebral and pleural ganglia; sub-pallial andro-diaulic or triaulic gonoduct system.[7] = Reduction of shell and mantle cavity, disintegration of head-shield with reduction of clypeo-capitis nerves; with subdermal spicule formations; reduction of right midgut gland; subpallial gonoduct; interstitial or/and limnic.[8] = Reduction of shell, mantle cavity, head-shield and nerves, jaws, radula, stomach, pericardium as well as heart; and pleural ganglia; with protonephridial system.[9] = Anterior gizzard with plates or teeth; sub-pallial gonoduct.[10] = Paedomorphy/neoteny (see p. 26) with heterostrophy of adult shell; pelagic life.[11] = Conservative group of Paratectibranchia with many retained plesiomorphic, but without (?) synapomorphic characters.[12] = Hypoathroid nervous system, oodiaulic genital system, disintegration of head-shield.[13] = Hypoathroid nervous system, reduction of shell and mantle cavity (with plicatidium retained?); pelagic camivory with buccal arms.[14] = Reduction of head-shield and clypeo-capitis nerves, reduction of mantle cavity but plicatidium retained.[15] = Shell flattened and circular in shape, or lost; jaws ring-shaped.[16] = Reduction of gizzard, osphradium, and albumen gland; blood gland close to the heart, cerebral nerves with accessory ganglia; chromosomes: n = 12.[17] = Larval shell dextrally coiled, adult shell orthostrophic; with bucco-pharyngeal acid gland.[18] = Reduction of shell, doridid shape; epidermis with so-called vacuole cells; right midgut gland small and on the right-anterior side; rhinophores retractile within sheaths; chromo-

somes: n = 13.[19] = Total detorsion (posteriomedian position of anus and excretory porus), gills in symmetric arrangement.[20] = Loss of plicatidium; fusion of cerebral and pleural ganglia.[21] = Characters of genus *Doridoxa*.[22] = No blood gland and bursa copulatrix; left midgut gland subdivided ('Cladohepatica').[23] = AEROPNEUSTA: Small animals without oralis nerves, with supplementary air-breathing; differentiation of procerebrum and cerebral glands; with pair of new peritentacular nerves but without rhinophoral nerves. Chromosomes: n = 16.[24] = *Gymnomorpha*: Reduction of shell, air-breathig with epidermis, mantle cavity restricted to a cloaca; retained (prosobranch) tentacles with eyes; procerebrum with globineurons only; genital system androdiaulic.[25] = Onchidiida: with secondary pulmonary space.[26] = Soleolifera: with soleolae, ureter gland for respiration, Semper's organ.[27] = *Pulmonata*: Air-breathing within mantle cavity (elaboration of a "lung") with pneumostome; head tentacles rudimentary, with eyes near base; procerebrum with both large cells and globineurons; single albumen gland.[28] = Siphonariidae, Amphibolidae, Trimus-culidae (Gadiniidae): independent offshoots of primitive pulmonate level, each sharing only certain symplesiomorphic characters (mantle cavity including osphradium, monauly, lack of tentacles (?), Veliger larva, or operculum).[29] = Hygrophila: with posttentacular sense organ, diaulic genital system; chromosomes: n = 18.[30] = Chilinoidea = Chilinidae and Latiidae: loss of anterior lobe of midgut gland; characters of each family.[31] = Branchiopulmonata: median eyes, osphradium outside of pneumostome, with ureter, loss of both vaginal vesicula and pulmonary caecum.[32] = Eupulmonata: Contractile pneumostome, distinct free tentacles, procerebrum with globineu-rons only, hypoarthroid nerve ring; chromosomes: n = 18.[33] = Ellobiidae and Otinidae: foot divided by transverse furrow; characters of each family (e.g. partial resorption of shell-lamella in Ellobiidae, or limpet shape with respiratory pedal lobes and alterations in the nervous system in Otinidae).[34] Head with retractile tentacles bearing the eyes, peritentacular nerves with outer branch, with ureter and podocyst.

---

is still accompanied by an external ciliated furrow, such as in *Chilina*; *cf*. HUBENDICK, 1978: 23/25). In contrast, the Pulmonata are characterized by the elaboration of the mantle cavity into a pulmonary organ with lung and pneumostome; basically no free tentacles appear to be present, and the genital system is monaulic. Gymnomorpha and Pulmonata, however, share the differentiation of a neurosecretory cerebral complex (procerebrum, cerebral gland, dorsal bodies), which demonstrates their monophyletic origin as Acropneusta (SALVINI-PLAWEN, 1990a).

Basommatophora possess a procerebrum with large nuclei in the cells, whereas Gymnomorpha and Stylommatophora with Ellobiidae show a procerebrum with small cells (globineurons).

HASZPRUNAR and HUBER (1990) interprete the latter condition (as well as the cloacal opening in Gymnomorpha and the contractile pneumostome in Stylommatophora) as synapomorphic; this is contradicted by VAN MOL (1967: 127-132, 1974) who cites convergency due to exclusive air-breathing. The primitive condition assumed by VAN MOL in Ellobiidae, however, is not in concordance with chromosome number (BURCH, 1960, 1967): Accordingly, the Siphorariidae (n = 16) exhibit the most primitive condition retained (see PATTERSON, 1967 for "mesogastropod" conditions). This is equally true of the extensive vascular plexus within the roof of the siphonariid mantle cavity, which simultaneously serves as a lung (YONGE, 1952; BRACE, 1983: 487). The chromosome

numbers contrast with those of other Basommatophora (n = almost exclusively 18) not to mention Stylommatophora (n = 20-34, except for Succineidae with n = 5-22); the Gymnomorpha (n = 16-18) are closest to Siphonariidae. This latter point is supported by sperm structure (HEALY, 1986). An evaluation of all these characters suggests the deviation of the Gymnomorpha already at the very root of the basommatophoran Pulmonata. This view was similarily expressed by HOFFMANN (1925: Fig. 40) and is accepted here. The relationships among Pulmonata (cf. HUBENDICK, 1947, 1978; MORTON, 1955; HARRY, 1964; VAN MOL, 1967, 1974; HASZPRUNAR & HUBER 1990) allow the Archaeopulmonata (Ellobiidae and Otinidae) to be aligned with the Stylommatophora: Eupulmonata (MORTON, 1955; emend. HASZPRUNAR & HUBER). In contrast, the Chilinoidea (Chilinidae and Latiidae) are close to the Branchiopulmonata (higher limnic Basommatophora): Hygrophila. Siphonariidae, Trimusculidae (Gadiniidae) and Amphibolidae represent primitive, thalassophile Pulmonata with disputed characters (e.g. patelliform shape, NS concentration) and ambiguous affinities.

2) Systematic survey of recent Mollusca

In concordance with the above remarks and argumentation, classification of molluscs (defined at p. 1, with primitive organization at p. 13) may be respectively adapted and outlined as follows (cf. Figs. 11, 13, 15; also SALVINI-PLAWEN, 1990a).

Class Caudofoveata (Chaetodermamorphs; mud moles): Worm-shaped Mollusca covered by cuticle and aragonitic scales; ventral gliding area reduced, mantle cavity terminal with one pair of ctenidia. Midgut with ventrally separated sac. Sexes separate. Adapted to burrowing habits in muddy sediments; marine in 10 - 7000 m 88 described species in a single order Chaetodermatida (three families); 2 mm - 14 cm in length (cf. SALVINI-PLAWEN, 1985).

Class Solenogastres (Ventroplicida, neomeniamorphs; narrowfoot gliders): Mollusca with narrowed body and gliding sole (foot), mantle with cuticle and aragonitic scales and/or spicules; mantle cavity modified, no true ctenidia; radula with pre-ribbon, midgut straight without separate glands. Hermaphroditic. Epibenthic predators of or epizoic on Cnidaria; marine, 5 - 6850 m. Some 185 described species in four orders (Pholidoskepia, Neomeniamorpha, Sterrofustia, Cavibelonia) according to characters of mantle cover (see Fig. 11); 0.8 mm - 30 cm in length (cf. SALVINI-PLAWEN, 1985).

Class Placophora (Polyplacophora, Loricata; chitons): Mollusca with generally flattened body and broad foot, mantle covered with cuticle and spicules, middorsally with eight serial shell plates (valves) enclosing photoreceptive papillae (aesthetes); mantle cavity peripedal with 8-88 pairs of ctenidia. Alimentary tract with esophageal and midgut glands, stomach, looped intestine. Marine, mainly algae-scraping on hard bottoms, 0 - 7000 m. About 600 recent species in three orders (Lepidopleurida, Chitonida = Ischnochitonida, Acanthochitonida), and Chelodida with fossil representatives only; 3 mm - 43 cm (cf. SALVINI-PLA-WEN, 1985).

Class Tryblidia (Monoplacophora or Galeroconcha partim; neopilinids): Mollusca-Conchifera covered by cap-shaped shell; head with two pairs of appendages, mantle cavity peripedal with 5-6 pairs of modified ctenidia; 5-6 pairs of excretory organs, two pairs of heart auricles and gonads. Marine detritus feeders, 175 - 6500 m; 12-15 species in one family, 1,5 mm - 37 mm (cf. WINGSTRAND, 1985; SALVINI-PLAWEN, 1988a).

Class Bivalvia (Pelecypoda, Acephala, Lamellibranchiata; clams/mussels/oysters/scallops/cockles): Mollusca-Conchifera with laterally compressed body, shell middorsally interrupted to form two hinged valves; posterior mantle often extended to form siphons; head with labial palps, foot axe-shape to vermiform, peri-pedal mantle cavity with one pair of ctenidia mostly modified into large plates of lamellae. Buccal mass (jaws and radula) reduced. Predominantly ciliary suspension feeders burrowing in mobile sediments or attached by byssus gland of foot to hard substrata; 0 - 10700 m. About 6000 marine and 2000 limnic species, 1 mm - 1.35 m in size. Three subclasses: Ctenidiobranchia (Nuculida), Palaeobranchia (Solemyida), Autobranchia (lamellibranch and septibranch bivalves) (cf. SALVINI-PLAWEN, 1980a; ALLEN, 1985). Among the latter, most successful

line only the Pteriomorpha (including the fili-
branch and pseudolamellibranch bivalves) are
synapomorphically delimited, and the Anomalo-
desmata (Pholadomyacea with Verticordiacea, and
Septibranchia) likewise appear to represent a well-
defined stock. Classification of other lamellibranch
bivalves, however, is still matter of discussion (*cf.*
ALLEN, 1985).

Class Scaphopoda (Solenoconcha; tusk shells):
Mollusca-Conchifera with midventrally fused
mantle and tubiform to barrelshaped shell. Head
with tubular snout and two bunches of slender
tentacles (captacula), foot pointed and cylindrical.
No ctenidia or distinct blood vessels, no heart-
auricles; radula strongly developed. Marine burro-
wers in mobile sediments, microcarnivores in 0 -
7000 m. About 350 species in two orders (Denta-
liida and Gadilida = Siphonodentaliida with sub-
orders Entaliphomorpha and Gadilimorpha; see
Fig. 13), 2 mm - 13.5 cm in length (*cf.* STEINER,
1990).

Class Gastropoda (Limpets, snails, slugs):
Mollusca-Conchifera basically with mantle cavity
shifted to anterior (torsion), sencondarily lateral to
terminal ("detorsion"); shell mostly coiled with
operculum, or rudimentary; head free with a pair
of photoreceptors. Left reproductive organs redu-
ced. About 40000 marine, limnic, and terrestrial
species in two subclasses; 0.3 mm - over 1 m in size
with an immense ecological and structural variabi-
lity.
Subclass STREPTONEURA: Predominantly
marine limpets or operculate snails; torsion pro-
nounced, with three ganglia in the visceral loop
(no parietal ganglia); two orders. Order *Archaeo-
gastropoda* with hypoathroid nervous system:
adjacent pleural and pedal ganglia, long cerebro-
pleural connectives; tentacles of head with simple
nerves, pedal ganglia with one commissure; six
suborders (Docoglossa, Cocculiniformia, Neritop-
sina, Vetigastropoda, Seguenziina, Architaenio-
glossa). Order *Apogastropoda* with epiarthroid
nervous system: adjacent cerebral and pleural
ganglia, cerebro-pleural connectives short; tenta-
cle nerve bifurcated, pedal ganglia with second =
parapedal commissure; larvae planktotrophic,
whith secondary shell; three suborders (Caenogas-
tropoda, Valvatina = Ectobranchia, Allogastropo-

da) (*cf.* SALVINI-PLAWEN & HASZPRUNAR, 1987;
HASZPRUNAR, 1988).
Subclass EUTHYNEURA: Marine, limnic, or
terrestrial snails and slugs with additional parietal
ganglia in the visceral loop (Pentaganglionata),
intercrossing of loop mostly anulled by concentra-
tion or reversion; primitively with folded secon-
dary gill (plicatidium) and marginal repugnatorial
glands; hermaphroditic. The subclass includes two
monophyletic lines (see Fig. 15):[1] The supraorder
Opisthobranchia includes the marine groups basi-
cally having the paired Hancock's sense organ or
their derivates with the respective innervation in
common (*see p. 22-23*). They may be classified
into Tectibranchia and Eleutherobranchia with
subgroups as discussed above (pp. 23-24 and Fig.
15). (2) The supraorder *Aeropneusta* includes
marine, limnic, and terrestrial shelled and naked
snails with synapomorphic procerebrum, cerebral
glands and dorsal bodies: Order Gymnomorpha
(mantle cavity reduced to a 'cloaca', or lost; loss of
shell; eyes pedunculated: Onchiida and Soleolife-
ra) and order Pulmonata (mantle cavity becomes a
'lung'; with subgroups as discussed p. 26 and
defined in Fig. 15).

Class Siphonopoda (Cephalopoda; nautiluses,
cuttle-fishes, squids, octopuses): Mollusca-Con-
chifera with dorso-ventrally elongated body; shell
straight, coiled, or regressive, originally chambe-
red and pierced by a siphuncular tube. Head free
with a pair of eyes and one or two circles of 8-10
or about 90 tentacles (perioral arms), foot modi-
fied as a funnel for jet propulsion, mantle cavity
restricted to posterior body with two or four cteni-
dia. Alimentary tract with strong jaws and predo-
minantly with a rectal ink sac; nervous system
extremely concentrated. About 600 recent species
(approximately 10000 fossil forms) measuring 1
cm - 8 m in body size (with arms up to 22 m);
basically marine carnivores, either pelagic from
the surface to 5400 m depth, or benthic to 8100 m.
Four subclasses:[1] Palcephalopoda (Orthoceroi-
da; fossil groups),[2] Nautiloida (fossil groups and
3-5 recent species),[3] Ammonoida (fossils only),
and (4) Coleoida with fossils and the three recent
orders Vampyromorpha, Octobrachia, and Deca-
brachia (including the suborders Spirulina, Myop-
seina with Sepioidea and Loliginoidea, and Oe-

gopseina) (cf. SALVINI-PLAWEN, 1980; BERTHOLD & ENGESER, 1987; TEICHERT, 1988; YOUNG, 1988).

ORIGEN, FILOGENIA Y CLASIFICACION DEL PHYLUM MOLLUSCA

Sinopsis

Dentro de los moluscos, tanto los Placofora como los Conchífera datan del Cámbrico Inferior (570-550 m. a.). El registro fósil, no obstante, arroja poca luz al objeto de esclarecer el *ORIGEN* de los moluscos y de dilucidar cómo pudo tener lugar anagenéticamente la diferenciación durante el Precámbrico de sus ocho clases existentes. Su evolución, por lo tanto, preferentemente ha de basarse en los datos de la anatomía comparada y de la ontogenia. Por otra parte, los datos procedentes de la Biología molecular son todavía ambiguos.

Teniendo presente los Caudofoveata y los Solenogastres, de los que no hay registro fósil y, cuyo estudio tradicionalmente ha sido negligido, la anatomía comparada de los moluscos sugiere que su punto de arranque común (los arquimoluscos), sin duda mostraban una configuración aplacófora. Su organización supondría: Locomoción ciliar, cavidad paleal, verosímilmente posterior en forma de U (con un par de ctenidios, tractos mucosos, etc.) y una posible nutrición a base de animales blandos. Los datos extraídos del desarrollo y de la reproducción permiten suponer que las larvas del tipo lecitotrófico (Pericalymma) con organización mesenquimática serían las primitivas. Estas relaciones parecen revelar preferentemente que los moluscos pudieron diferenciarse, más bien a partir de organismos diminutos (1-5 mm de tamaño) con organización platelmintomorfa que habrían esbozado una cubierta paleal, que a partir de organismos fosores celomados (segmentados o no).

A lo largo de la *FILOGENIA,* el acontecimiento más.obvio de la radiación evolutiva de los moluscos lo constituye el desarrollo de la cubierta paleal que defina los niveles de organización aplacófora, poliplacófora y (por integración) monoplacófora. Esta secuencia es concomitante con la regresión de los sistemas musculares subpaleal y longitudinal-marginal y con la concentración progresiva de la musculatura dorsoventral. Los Caudofoveata y los Solenogastres en virtud de la configuración del manto y la cavidad paleal reflejan dos líneas parafiléticas separadas. Los Solenogastres, esencialmente carnívoros, parecen estar relacionados por ciertos rasgos de su desarrollo con los Placofora, si bien han conservado el tracto digestivo arcaico (con membrana radular rudimentaria, intestino medio sacciforme y voluminoso sin glándula digestiva disociada). Este último, en los Placófora se diferencia en: faringe, esófago provisto de un par de sacos glandulares, estómago con un par de glándulas digestivas e intestino delgado; organización ésta, que será transmitida al nivel monoplacóforo (= Conchífera). Así mismo, el órgano subradular, la doble disposición octoserial de la musculatura dorsoventral, la estructura trilaminar de la concha que incluye papilas paleales, así como el sistema excretor (los emuntorios) constituyen la prueba del legado poliplacóforo de los Tryblidia ("Monoplacophora"), los cuales representan el nivel más primitivo de los Conchifera. Las limitaciones metabólicas inherentes al hábito adhesivo, característico de los Placophora vivientes, determinaron fenómenos selectivos que motivaron el aumento del número de ctenidios y la prolongación anterior de los órganos emuntorios. Similarmente, el confinamiento de los Tryblidia actuales en "hábitats refugio" explicará no sólo la multiplicación de los ctenidios, sino también la división del corazón y la subdivisión de los emuntorios. Una vez formados los Conchifera primitivos, dotados ya de tentáculos cefálicos, formaciones mandibulares, estómago provisto de un saco portador de proto-estilo, estatocistos y comisura visceral subrectal, se habrían escindido en las dos líneas anagenéticas actualmente existentes:

(1) Los Loboconcha (o Diasoma), donde se incluyen los Bivalvia y los Scaphopoda, así como su eslabón intermedio, los extinguidos Rostroconcha, que muestran el manto y la concha expandidos lateralmente envolviendo las partes blandas, y un pie anterior alargado, bien adaptado para vivir en fondos blandos.

(2) Los Visceroconcha, que incluyen los Gastropoda (marcados por la torsión) y los Siphonopoda (impropiamente denominados Cefalopoda, pues sus brazos prensores presentan una inervación predominantemente cerebral, más que pedal) están provistos de cabeza individualizada (con fotoreceptores cerebrales), separada de la masa visceral recubierta por el manto y protegido por la

concha, cavidad paleal posterior, cordones nervio-
sos laterales/pleurales emplazados mesialmente
con relación a la musculatura dorsoventral, y un
sistema muscular antagónico tridimensional de
músculos correlativos.

En lo que concierne a la *CLASIFICACION,* los
descubrimientos actuales y la reconsideración de
los datos de la organización interna sobre los
diferentes grupos de moluscos revelan varios
aspectos nuevos esenciales. Estos implican ciertos
cambios en la sistemática de los Scaphopoda, de
los Bivalvia y de los Siphonopoda, aunque las
consecuencias más decisivas se refieren a la reor-
ganización sistemática de los Gastropoda. Por úl-
timo, los términos "Aplacophora", "Amphineura"
y "Protobranchia" actualmente carecen de valor
taxonómico.

ACKNOWLEDGEMENT

BIBLIOGRAPHY

ALLEN, J.A. 1985. The recent Bivalvia: Their form and evolution. *The Mollusca.* Acad. Press, 10 (Evolution): 337-403.

ANDREWS, E. 1988. Excretory systems of Molluscs. *The Mollusca.* Acad. Press, 11 (Form and Function): 381-448.

BABA, K. 1940. The mechanisms of absorption and excretion in a solenogastre, *Epimenia verrucosa* (NIERSTRASZ), studied by means of infection methods. *Journ. Dept. Agriculture Kyusyu Imp. Univ.,* 6(4): 119-166.

BANDEL, K. 1982. Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. *Facies,* 7: 1-198.

BARNES, R.S.K., CALOW, P. & OLIVE, P.J.W. 1988. *The Invertebrates: a new systhesis.* Blackwell Sci. Publ., Oxford, 582 p.

BARTHOLOMAEUS, Th., 1990. Zur Ultrastruktur und Entwicklung der Nephridien bei Annelida und ihrer phylogenetischen Bewertung. Verhandl. *Dtsch. Zoll. Ges.* 83: 502-503.

BERGSTRÖM, J. 1986. Metazoan evolution — a new model. *Zool. Scripta,* 15: 189-200.

BERTHOLD, Th. & ENGESER, Th. 1987. Phylogenetic analysis and systematization of the Cephalopoda (Mollusca). *Verh. naturwiss. Ver. Hamburg,* (NF), 29: 187-220.

BOSS, K. 1971. Critical estimate of the number of recent Mollusca. *Occas. Pap. Moll.,* 3(40): 81-135.

BOSS, K. 1982. Mollusca. In: *Synopsis and classification of living organisms.* S.B. Parker, McGraw-Hill, New York, 1: 945-1166.

BRACE, R. 1983. Observations on the morphology and behaviour of *Chilina fluctuosa* GRAY (Chilinidae), with discus-

sion on the early evolution of pulmonate gastropods. *Phil. Transact. Roy. Soc. London.,* B 300: 463-491.

BRIGGS, D.E.G., ALDRIDGE, R.J. y SMITH, M.P. 1987. Conodonts are not aplacophoran molluscs. *Lethaia,* 20: 381-382.

BROWN, A.C., TRUEMAN, E.R. & STENTON-DOZEY, J. 1989. Gill size and respiratory requirement in the Mollusca, with special reference to the prosobranch Gastropoda. *South African Journ. Sci.,* 85: 126-127.

BROWN, H.H. 1934. A study of a tectibranch gastropod mollusc, *Philine aperta* (L.). *Transact. Roy. Soc. Edinburg.,* 58: 179-210.

BURCH, J.B. 1960. Chromosome morphology of aquatic pulmonate snails (Mollusca: Pulmonata). *Transact. Amer. Microsc. Soc.,* 79: 451-461.

BURCH, J.B. 1967. Cytological relationships of some Pacific gastropods. *Vesnus,* 25: 118-135.

CHAFFEE Ch. & LINDBERG, D.R. 1986. Larval biology of early Cambrian molluscs: the implications of small body size. *Bull. mar. Sci.,* 39: 536-549.

CHANLEY, P. 1969. Larval development in the class Bivalvia. *Mar. biol. Ass. India, Proc. Symp.,* 3 (Moll.), (2): 475-481.

CLARK, R.B. 1964. *Dynamic in metazoan evolution: the origin of the coelom and segments.* Clarendon Press, Oxford, 313 p.

CLARK, R.B. 1979. Radiation of the Metazoa. *Syst. Ass., spec.,* Vol. 12 (The origin of major invertebrate groups): 55-102.

CONWAY MORRIS, S. 1985. The Middle Cambrian metazoan *Wiwaxia corrugata* (Matthew) from the Burgess Shale and *Ogygopsis* Shale, British Columbia, Canada. *Phil. Transact. Roy. Soc. London,* B 307 (1134): 507-586.

CONWAY MORRIS, S. & PEEL, J.S. 1990. Articulated halkieriids from the Lower Cambrian of north Greenland. *Nature,* 345(6278): 802-805.

CROFTS, D. 1937. The development of *Haliotis tuberculata.* *Phil. Transact. Roy. Soc. London,* B 228: 129-268.

DELL'ANGELO, B. 1982. Sui casi di anomali del numero di piastre dei Polyplacophora. *Boll. malacol.,* 18: 235-246.

DREW, G.A. 1901. The life-history of *Nucula delphinodonta.* *Quart. Journ. Micr. Sci.,* 44: 313-391.

EMSCHERMANN, P. 1969. Ein Kreislauforgan bei Kamptozoen. *Zeit-schr. Zellforsch.,* 97: 576-607.

ERDMANN, W. 1934. Untersuchiungen über die Lebensgeschichte der Auster Nr. 5. *Wiss. Meeresunters.* (Helgoland) NF 19(3/6): 1-25.

FIELD, K.G., OLSEN, G., LANE, D., GIOVANNONI, St., GHISELIN, M., RAFF, E., PACE, N. & RAFF, R. 1988. Molecular phylogeny of the Animal Kingdom. *Science,* 329: 748-753.

FIORONI, P. 1966. Zur Morphologie und Embryogenese des Darmtraktes und der transitorischen Organe bei Prosobranchiem (Mollusca, Gastropoda). *Revue Suisse Zool.,* 73: 621-876.

FIORONI, P. 1982. Larval organs, larvae, metamorphosis and types of development of Mollusca — a comprehensive review. *Zool. Jahrb. Anat.,* 18: 375-420.

FISCHER, F. 1978. Photoreceptor cells in chiton aesthetes (Mollusca, Polyplacophora, Chitonidae). *Spixiana,* 1: 209-213.

FRANZEN, A. 1956. On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. *Zool. Bidr. Uppsala,* 31: 355-482.

FRANZEN, A. 1970. Phylogenetic aspects of the morphology of the spermatozoa and spermiogenesis. In: *Comparative Spermatology.* Baccetti, B., edit., Acad. Press., 29-46 pp.

FRETTER, V. 1943. Studies in the functional morphology and embryology of *Onchidella celtica* (Forbes and Hanley) and their bearing on its relationships. *Journ. mar. biol. Ass. U.K.*, 25: 685-720.

FRETTER, V. & GRAHAM, A. 1962. *British prosobranch molluscs*. Ray Society, London, 755 p.

GASCOIGNE, T. & SARTORY, P.K. 1974. The teeth of three bivalved gastropods and three other species of the order Sacoglossa. *Proc. malac. Soc. London*, 41: 109-124.

GHISELIN, M.T. 1966. Reproductive function and phylogeny of opisthobranch gastropods. *Malacologia*, 3(3): 327-378.

GHISELIN, M.T. 1988. The origin of molluscs in the light of molecular evidence. *Oxford Surveys evol. Biol.*, 5: 66-95.

GLAESSNER, M. 1969. Trace fossils from the Precambrian and basal Cambrian. *Lethaia*, 2: 369-393.

GREEN, C.R. & BERGQUIST, P.R. 1982. Phylogenetic relationships within the Invertebrata in relation to the structure of septate junctions and the development of 'occluding' junctional types. *Journ. Cell. Sci.*, 53: 279-305.

GÖTTING, K.-J.. 1980. Argumente für die Deszendenz der Mollusken von metameren Antezedenten. *Zool. Jahrb. Anat.*, 103: 211-218.

GUTMANN, W.F. 1974. Die Evolution der Mollusken-Konstruktion: ein phylogenetisches Modell. *Aufsätze Reden Senckenb. naturf. Ges.*, 25: 1-84.

HAAS, W. 1981. Evolution of calcareous hardparts in primitive molluscs. *Malacologia*, 21: 403-418.

HADL, G., H. DOTHBAVER, R. PETER & E. WAWRA, 1970. Substratwahlversuche mit *Microhedyle milaschewitchii* Kowalevsky (Gastropoda, Opisthobranchia: Acochlidiacea). *Oecologia (Berlin)*, 4: 74-82.

HAMMARSTEN, O. & RUNNSTRÖM, J. 1926. Zur Embryologie von *Acanthochiton discrepans* BROWN. *Zool. Jahrb. Anat.*, 47: 261-318.

HARRY, H.W. 1964. The anatomy of *Chilina fluctuosa* Gray reexamined, with prolegomenaqa on the phylogeny of the higher limnic Basommatophora (Gastropoda: Pulmonata). *Malacologia*, 1(3): 355-385.

HASZPRUNAR, G. 1985a. The Heterobranchia — a new concept of the phylogeny of the higher Gastropoda. *Zeitschr. zool. Syst. Evolut.-forsch.*, 23: 15-37.

HASZPRUNAR, G. 1985b. The fine morphology of the osphradial sense organs of the Mollusca. I. Gastropoda, Prosobranchia. *Phil. Transact. Roy. Soc. London*, B 307: 457-496.

HASZPRUNAR, G. 1987a. The fine morphology of the osphradial sense organs of the Mollusca. III. Placophora and Bivalvia. *Phil. Transact. Roy. Soc. London*, B 315: 37-61.

HASZPRUNAR, G. 1987b. The fine morphology of the osphradial sense organs of the Mollusca. IV. Caudofoveata and Solenogastres. *Phil. Transact. Roy. Soc. London*, B 315: 63-73.

HASZPRUNAR, G. 1988. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Journ. moll. Stud.*, 54: 367-441.

HASZPRUNAR, G. & HUBER, G. 1990. On the central nervous system of Smeagolidae and Rhodopidae, two families questionably allied with the Gymnomorpha (Gastropoda: Euthyneura). *Journ. Zool. (London)*, 220: 185-199.

HEALY, J. 1986. Electron microscopic observations on the spermatozoon of a marine "pulmonate" slug, *Onchidium damelli* (Gastropoda, Onchidiacea). *Journ. submicrosc. Cytol.*, 18: 587-594.

HEATH, J. 1899. The development of *Ischnochiton*. *Zool. Jahrb. Anat.*, 12: 567-656.

HENDRIKS, A., HUYSMANS, E., VANDENBERGHE, A. & DE WACHTER, R. 1986. Primary structures of the 5S RNA to the study of metazoan evolution. *Journ. mol. Evol.*, 24: 103-109.

HIGLEY, R. & HEATH, H. 1912. The development of the gonad and gonoducts in two species of chitons. *Biol. Bull. (Woods Hole)*, 22: 94-97.

HOFFMANN, H. 1925. Die Vaginuliden. *Jena. Zeitschr. Naturwiss*, 61: 1-374.

HOFFMANN, H. 1937. Über die Stammesgeschichte der Weichtiere. *Zool. Anz.*, Suppl. 10: 33-69.

HOFFMANN, H. 1938. Opisthobranchia 3. In: *Bronns Klass. Ordn. Tierreich* III/2, 3/I (1,4): 865-1104.

HOFFMAN , S. 1949. Studien über das Integument der Solenogastren, nebst Bemerkungen über die Verwandtschaft zwischen den Solenogastres und Placophoren. *Zool. Bidr. Uppsala*, 27: 293-427.

HUBENDICK, B. 1947. Phylogenie und Tiergeographie der Siphonariidae. *Zool. Bidr. Uppsala*, 24: 1-216.

HUBENDICK, B. 1978. Systematics and comparative morphology of the Basommatophora. In: *Pulmonates*, Fretter, V. & Peake, J., eds., Acad. Press, 2: 1-48.

HUBER, G. 1987. Zum cerebralen Nervensystem mariner Heterobranchia (Gastropoda). *Diss. Formal- & naturwiss. Fak. Univ. Wien*, 168 p.

HYMAN, L. 1951. The acoelomate Bilateria - Phylum Plathelminthes. *The Invertebrates* II: 52-458.

IHERING, H.v. 1922. Phylogenie und System der Mollusken. *Abhandl Archiv, Molluskenkunde*, 1: 1-116.

JABLONSKI, D. & LUTZ, R.A. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biol. Rev.*, 58: 21-98.

JAECKEL, S., 1952. Zur Verbreitung und Lebensweise dr Opisthobranchier in der Nordsee. *Kieler Meeresforsch.* 8: 249-259.

KERTH, K. 1983. Radulaapparat und Radulabildung der Mollusken II. *Zool. Jahrb. Anat.*, 110: 239-269.

KOWALEVSKY, A. 1883a. Embryogénie du *Chiton polii* (PHILIPPI). *Ann. Mus. Hist. Nat. Marseille, Zool.*, 1(5): 1-46.

KOWALEVSKY, A. 1883b. Etude sur l'embryogénie du Dentale. *Ann. Mus. Hist. Nat. Marseille, Zool.*, 1(7): 1-54

LANGER, P. 1978. Abnormality of shell plates in three chitons from New England. *The Veliger*, 21: 274-275.

LEMCHE, H. & WINGSTRAND, K. 1959. The anatomy of *Neopilina galatheae* LEMCHE, 1957 (Mollusca, Tryblidiacea). *Galathea Report*, 3: 9-72.

LIMA, G.M. & LUTZ, R.A. 1990. The relationship of larval shell morphology to mode of development in marine prosobranch gastropods. *Journ. mar. biol. Ass. U.K.*, 70: 611-637.

LYDDIATT, A., PEACOCK, D. & BOULTER, D. 1978. Evolutionary change in invertebrate cytochrome C. *Journ. mol. Evol.*, 11: 35-45.

MANTON, S. & ANDERSON, D.T. 1979. Polyphyly and the evolution of arthropods. *Syst. Ass., spec.*, Vol. 12 (The origin of major invertebrate groups): 269-321.

MARCUS, E. 1953. Three Brazilian sand-Opistobranchia. *Bol. Fac. Fil. Cienc. Univ. Sao Paulo*, 165(Zool. 18): 165-203.

MARCUS, E.D.B.-R. 1982. Systematics of the genera of the order Ascoglossa (Gastropoda). *Journ. Moll. Stud.*, Suppl. 10: 1-31.

MARTIN, A.W. 1983. Excretion. *The Mollusca*. Acad. Press, 5

(Physiology 2): 353-405.

MINICHEV, Yu. & SIRENKO, B. 1984. Formation of metameric organs during the ontogenesis of chitons. *Malacol. Review*, 17 (1-2): 111

MINICHEV, Yu. & STAROBOGATOV, Y. 1972. The problem of torsion process and promorphological rearrangement in larvae of trochophore animals. *Zool. Zhurn.*, 51(10): 1437-1449 (in Russian).

MORTON, J.E. 1955. The evolution of the Ellobiidae with a discussion of the Pulmonata. *Proc. Soc. Zool. London*, 125: 127-168.

ODHNER, N.H. 1937. *Hedylopsis suecica* n. sp. und die Nackschneckengruppe Acochlidiacea (Hedylacea). *Zool. Anz.*, 120: 51-64.

OLIVE, P.J.W. 1985. Covariability of reproductive traits in marine invertebrates: implications for the phylogeny of the lower invertbrates. *Syst. Ass., spec.*, Vol. 28: (The origins and relationships of lower invertebrates): 42-59.

PATTERSON, C.M. 1967. Chromosome numbers and systematics in streptoneuran snails. *Malacologia*, 5: 111-125.

PETERS, W. 1972. Occurrence of chitin in Mollusca. *Comp. Biochem. Physiol.*, 41B: 541-550.

POJETA, J. & RUNNEGAR, B. 1976. The paleontology of rostroconch mollusks and the early history of the phylum Mollusca. *U.S. Geol. Survey prof. Pap.*, 968: 1-88.

PRUVOT, G. 1890. Sur le développement d'un Solenogastre. *C.R. Acad. Sci. Paris,* 111(2): 689-692.

RAVEN, Ch. 1958. The analysis of molluscan development. *Morphogenesis.* Pergamon Press, 2: 1-311.

RIEGER, R. 1984. Evolution of the cuticle in the lower Eumetazoa. Biology of the Integument (Springer-Verlag), 1 *Invertebrates*: 389-399.

RIEGER, R. & STERRER, W. 1975. New spicular skeletons in Turbellaria and the occurrence of spicules in marine meiofauna, II. *Zeitschr. zool. Syst. Evolut.-forsch.*, 13: 249-278.

ROLFE, W. 1981. *Septemchiton* —a misnomer. *Journ. Paleontology,* 55: 675-678.

RUNNEGAR, B. & POJETA, J. 1985. Origin and diversification of the Mollusca. *The Mollusca.* Acad. Press, 10 (Evolution): 1-57.

RUSSEL-HUNTER, W.D. 1988: The gills of chitons (Polyplacophora) and their significance in molluscan phylogeny. *Amer. malacol. Bull.*, 6 (1): 69-78.

SALVINI-PLAWEN, L.v. 1968. Die 'Funktions-Coelomtheorie' in der Evolution der Mollusken. *Syst. Zool.*, 17: 192-208.

SALVINI-PLAWEN, L. v. 1970. *Phyllomenia austrina,* ein phylogenetisch bedeutsamer Solenogaster (Mollusca, Aculifera). *Zeitschr. zool. Syst. Evolut.-forsch.*, 8: 297-309.

SALVINI-PLAWEN, L.v. 1972. Zur Morphologie und Phylogenie der Mollusken. *Zeitschr. wiss. Zool.*, 184: 205-394.

SALVINI-PLAWEN, L.v. 1978. Antarktische und subantarktische Solenogastres (Eine Monographie: 1898-1974): *Zoologica (Stuttgart)*, 128: 1-315.

SALVINI-PLAWEN, L.v. 1980a. A reconsideration of systematics in Mollusca (Phylogeny and higher classification). *Malacologia*, 19 (2): 247-278.

SALVINI-PLAWEN, L.v. 1980b. Was ist eine Trochophora? - Eine Analyse der Larventypen mariner Protostomier. *Zool. Jahrb. Anat.*, 103: 389-423.

SALVINI-PLAWEN, L.v. 1981a. On the origin and evolution of the Mollusca. *Atti Convegni Lincei*, 49: 235-293.

SALVINI-PLAWEN, L.v. 1981b. The molluscan digestive system in evolution. *Malacologia*, 21: 371-401.

SALVINI-PLAWEN, L.v. 1985. Early evolution and the primitive groups. *The Mollusca.* Academic Press, 10 (Evolution): 59-150.

SALVINI-PLAWEN, L.v. 1986. The status of Rhodopidae (Gastropoda: Euthyneura). *Abstr. 9th Int. Malacol. Congr. Edinburgh:* 76.

SALVINI-PLAWEN, L.v. 1988a. The structure and function of molluscan digestive systems. *The Mollusca.* Acad. Press, 11 (Form and Function): 301-379.

SALVINI-PLAWEN, L.v. 1988b. Annelida and Mollusca - a prospectus. *Microfauna marina*, 4: 383-396.

SALVINI-PLAWEN, L.v. 1990a. Mollusks. *The new Encyclopaedia Britannica*, 24: 306-311.

SALVINI-PLAWEN, L.v. 1990b. The status of the Caudofoveata and the Solenogastres in the Mediterranean Sea. *Lavori SIM*, 23: 5-30.

SALVINI-PLAWEN, L.v. 1990c. The status of the Rodopidae (Gastropoda: Euthyneura). *Ninth int. malacol. Congr. (Edinburgh) Symp.*, 1 (Evolutionary Biology of Opisthobranchs): 123-136.

SALVINI-PLAWEN, L.v. & HASZPRUNAR, G. 1987. The Vetigastropoda and the systematics of streptoneurous Gastropoda (Mollusca). *Journ. Zool. London*, 211: 747-770.

SARASIN, P. & SARASIN, F. 1899. Die Landmollusken von Celebes. Materialien Naturgesch. *Celebes (C.W. Kreidel, Wiesbaden)*, 2: 1-248.

SCHELTEMA, A. 1978. Position of the class Aplacophora in the phylum Mollusca. *Malacologia*, 17: 99-109.

SCHELTEMA, A. 1981. Comparative morphology of the radulae and alimentary tracts in the Aplacophora. *Malacologia*, 20: 361-383.

SCHELTEMA, A. 1988. Ancestors and descendents: relationships of the Aplacophora and Polyplacophora. *Amer. malacol. Bull.*, 6 (1): 57-68.

SCHMEKEL, L. 1985. Aspects of evolution within the opisthobranchs. *The Mollusca.* Acad. Press, 10 (Evolution): 221-267.

SCHMEKEL, L. & PORTMANN, A. 1982. Opisthobranchia des Mittelmeeres (Nudibranchia und Saccoglossa). *Fauna Flora Golfo Napoli*, 40: 1-410.

SHUTO, T. 1974. Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. *Lethaia*, 7: 239-256.

SIRENKO, B. & MINICHEV, Y. 1975. Developpement ontogenetique de la radula chez les Polyplacophores. *Cah. Biol. mar.*, 16: 425-433.

SMITH, A.B. 1989. RNA sequence data in phylogenetic reconstruction: testing the limits of its resolution. *Cladistics*, 5: 321-344.

STASEK, Ch.R. 1972. The molluscan framework. *Chemical Zoology*, 7: 1-44.

STEINER, G. 1990. Beiträge zur vergleichenden Anatomie und Systematik der Scaphopoda (Mollusca). *Diss. Formal- & naturwiss. Fak. Univ. Wien* (N 1006), 176 p.

TAKI, I. 1932. On some cases of abnormality of the shellplates in chitons. *Mem. Coll. Sci., Kyoto Imp. Univ.*, (ser. B), 8: 27-64.

TARDY, J. 1970. Contributions à l'études metamorphoses chez les nudibranches. *Ann. Sci. Nat. Zool. et Biol.*, 12: 299-370.

TEICHERT, C. 1988. Main features of cephalopod evolution. *The Mollusca.* Acad. Press, 12 (Paleontology and neontology of cephalopods): 11-79.

TERWILLIGER, R.C. 1980. Structures of invertebrate

haemoglobins. *Amer. Zool.*, 20: 53-67.

THOMSON, T.E. 1960. The development of *Neomenia carinata* Tullberg. *Proc. Roy. Soc. London*, 153B: 263-278.

THOMSON, T.E. 1979. Biology and relationships of the South African sacoglossan mollusc *Volvatella laguncula. Journ. Zool. (London)*, 189: 339-347.

TILLIER, S. & CUIF, J.-P. 1986. L'animal conodonte est-il un Mollusc aplacophore? *C.R. Seances Acad. Sci.*, (ser. II), 7: 627-632.

TILLIER, S. & JANVIER, P. 1986. Le retour de l'animal-conodonte. *La Recherche*, 17: 1574-1575.

TRUEMAN, E.R. 1975. *The locomotion of soft-bodied animals*. Edward Arnold, London, 200 p.

TRUEMAN, E.R. & BROWN, A.C. 1985. The mechanism of shell elevation in *Haliotis* (Mollusca: Gastropoda) and a consideration of the evolution of the hydrostatic skeleton in Mollusca. *Journ. Zool. London (a)*, 205: 585-594.

TSCHERKASSKY, M., 1989. Pedal shield or oral shield in Caudofoveata (Mollusca, Aculifera)? *Abstr. 10th Int. Malacol. Congr. Tübingen*: 254.

VAGVOLGYI, J. 1967. On the origin of the molluscs, the coelom and the coelomatic segmentation. *Syst. Zool.* 16: 153-168.

VAN MOL, J.-J. 1967. Etude morphologique et phylogénetique du ganglion cerebroide des Gastéropodes pulmonés (Mollusques). *Mem. Acad. roy. Belgique, Cl. Sci.*, Ser. 2, 37(5): 1-168.

VAN MOL, J.-J. 1974. Evolution phylogénetique du ganglion cerebroide chez les Gasteropodes pulmonés. *Haliotis*, 4: 77-86.

WÄGELE, H. 1989. Die Gattung *Bathydoris* Bergh, 1884 (Gnathodoridacea) im phylogenetischen System der Nudibranchia (Opisthobranchia, Gastropoda). *Zeitschr. zool Syst. Evolut.-forsch.*, 27: 273-281.

WERNER, B. 1955. Über die Anatomie, die Entwicklung und Biologie des Veligers und der Veliconcha von *Crepidula fornicata* L. (Gastropoda, Prosobranchia). *Helgoländer wiss. Meeresunters.* 5 (2): 169-217.

WILHELMI, R.W. 1944. Seriological relationships between the Mollusca and other invertebrates. *Biol. Bull.*, 87: 96-105.

WILLAN, R.C. 1987. Phylogenetic systematics of the Notaspidea (Opisthobranchia) with reappraisal of families and genera. *Amer. malacol. Bull.*, 5: 215-241.

WILLMER, P. 1990. *Invertebrate Relationships. Patterns in animal evolution*. Cambridge Univ. Press, Crambidge, 400 p.

WINGSTRAND, D.G. 1985. On the anatomy and relation-ships of recent Monoplacophora. *Galathea Report*, 16: 7-94.

WIRTH, U. 1984. Die Struktur der Metazoen-Spermien und ihre Bedeutung für die Phylogenetik. *Verhandl. naturwiss. Verein Hamburg NF*, 27: 295-362.

WOLTER, K. 1991. Ultrastructural investigations of the radula apparatus in some species of aplacophoran molluscs. *Journ. moll. Stud.*, (in press).

YONGE, C.M. 1947. The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Phil. Transact. Roy. Soc. London*, 232(B 591): 443-517.

YONGE, C.M. 1952. The mantle cavity in *Siphonaria alternata* SAY. *Proc. malac. Soc. London*, 29: 190-199.

YOUNG, J.Z. 1977. Brain, behaviour and evolution of cephalopods. *Symp. zool. Soc. London*, 38: 377-434.

YOUNG, J.Z. 1988. Evolution of the cephalopod brain. *The Mollusca*. Acad. Press, 12 (Paleontology and Neontology of cephalopods): 215-228.

YU, W. 1984. On Merismoconchids. *Acta palaeontol. sinica*, 23 (4): 432-446.

YU, W. 1987. Yangtze micromolluscan fauna in Yangtze region of China with notes on Precambrian-Cambrian boundary. Stratigraphy and Paleontology boundary in China Precambrian-Cambrian Boundary. *Nanjing Inst. Geol. Palaeont., Acad. Sinica, Nanjing Univ. Publ.*, 1: 19-275.